

Mollusca Cephalopoda: Mid-depth octopuses (200-1000 m) of the Banda and Arafura Seas (Octopodidae and Alloposidae)

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ABSTRACT

Six mid-depth octopuses of the Order Octopoda are reported from the Banda and Arafura Seas off Indonesia and northern Australia, based on material collected through the collaborative French-Indonesian KARUBAR cruise of 1991. Octopod material was collected through benthic trawls at 18 of 91 stations, at depths between 199 and 869 metres. Two new species are described here, *Benthioctopus karubar* sp. nov. and *Octopus pyrum* sp. nov. An additional species of the genus *Octopus* is reported as indeterminate but distinct from *O. pyrum*. The genus *Pteroctopus* is reported from Indo-Pacific waters for the first time, based on female material collected through the KARUBAR cruise and linked with additional male material collected off New Caledonia and Vanuatu. *Eledone palari* is recorded as a northerly extension to the Australian distribution reported in the original description for this species. A single submature female of the pelagic octopod, *Haliphron atlanticus* (previously treated under the name *Alloposus mollis*), is also reported from the region. The depth distributions and phylogenetic affinities of this fauna are discussed.

RÉSUMÉ

Mollusca Cephalopoda ; Pieuvres bathyales (200-1000 m) des mers de Banda et d'Arafura (Octopodidae et Alloposidae).

La campagne franco-indonésienne KARUBAR dans les mers de Banda et d'Arafura, au large de l'Indonésie et du nord de l'Australie, a permis la capture de six espèces de pieuvres de l'ordre des Octopoda dans 18 des 91 stations prospectées entre

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199 et 869 mètres de profondeur. Deux espèces nouvelles sont décrites : *Benthoctopus karubar* sp. nov. et *Octopus pyrum* sp. nov. Une autre espèce d'*Octopus*, distincte d'*O. pyrum*, est présente, mais reste indéterminée. Le genre *Pteroctopus* est signalé pour la première fois du domaine indo-pacifique sur la base d'une femelle récoltée pendant la campagne KARUBAR, et ce matériel est conspécifique avec des individus mâles récoltés en Nouvelle-Calédonie et au Vanuatu. La présence d'*Eledone palari* en mer d'Arafura étend un peu au nord l'aire de distribution connue de cette espèce, récemment décrite d'Australie. Enfin, l'octopode pélagique *Haliphron atlanticus* (plus connu sous le nom *Alloposus mollis*) est également représenté par un seul individu, une femelle pré-mature. La répartition bathymétrique et les affinités phylogénétiques de cette faune sont discutées par rapport à celles d'Australie et du reste de l'Indo-Pacifique.

INTRODUCTION

The octopod fauna of the tropical Indo-West Pacific region is still poorly known, despite many species having high profiles in commercial and subsistence fisheries. Recent research into shallow-water octopuses of this region, particularly the Indo-Malayan region, has encountered a diverse, largely undescribed fauna (NORMAN, 1992a, 1992b, 1993a, 1993b, 1993c, 1993d; NORMAN & HOCHBERG, 1994; NORMAN & SWEENEY, 1997; NORMAN, in press).

Octopuses from beyond the continental shelves (> 200 m) in the Indo-West Pacific have received even less attention than shallow taxa. This is a product of the few deep-water surveys undertaken in this region and/or the limited retention of cephalopod material on such cruises. The expeditions of the "*Dana*" (THORE, 1949) and "*Siboga*" (ADAM, 1954) are two of the few exceptions. ROBSON (1925, 1932), VOSS (1967, 1988a, 1988b) and NESIS (1987) provided reviews of deeper sea octopods of the world, collating available information on animals found at such depths. These authors recognised that the majority of described species are based on limited (often poorly preserved) material, from few stations. Few works have provided detailed morphological comparison of species occurring in deeper waters [exceptions being VOSS & PEARCY (1990) and LU & STRANKS (1994)].

In 1991, French-Indonesian collaboration resulted in the KARUBAR research cruise to the Banda and Arafura Seas. A series of 91 benthic trawl stations were carried out employing the Indonesian research vessel, "*Baruna Jaya I*", at depths between 100 and 1250 metres. Material collected through this cruise is lodged in the collections of the Muséum National d'Histoire Naturelle, Paris (MNHN) and the Puslitbang Oseanologi - LIPI, Jakarta (POLIPI).

In a visit to the Paris museum by the first two authors in November 1995, octopod material collected through the KARUBAR cruise was examined. Benthic (incirrate) octopuses originated from 18 stations at depths ranging between 199 and 869 metres. Finned octopods (Cirroctopoda) were also encountered at a number of stations and this material will be treated elsewhere.

MATERIAL AND METHODOLOGY

Trawls were carried out on board the "*Baruna Jaya I*" from October 22 to November 5, 1991. Four gear types were employed of which 3 captured octopods: Waren dredge, (Drague Waren, station code: DW), Beam trawl (chalut à perche, station code: CP) and shrimp trawl (chalut à panneaux [crevettes], station code: CC). All molluscs collected in these trawls (including cephalopods) were separated on board by P. BOUCHET, W. KASTORO and B. MÉTIVIER.

Octopod material was collected from 18 KARUBAR stations. Locality details for these stations are provided in Table 1 (p. 379). Type material for the 2 new species described here are lodged in the cephalopod collections of the Muséum National d'Histoire Naturelle (MNHN), Paris, the Puslitbang Oseanologi - LIPI (POLIPI), Jakarta and the Museum of Victoria (MV), Melbourne.

Morphological characters and measurements used in the descriptions below are illustrated in Figure 1. Gill counts refer to the number of lamellae on each side of each gill (= per *demibranch*, an inner and outer demibranch on each gill). Count per demibranch excludes central terminal (anterior) lamella, e.g., animals illustrated in Figures 1e-f have a gill count of 10.

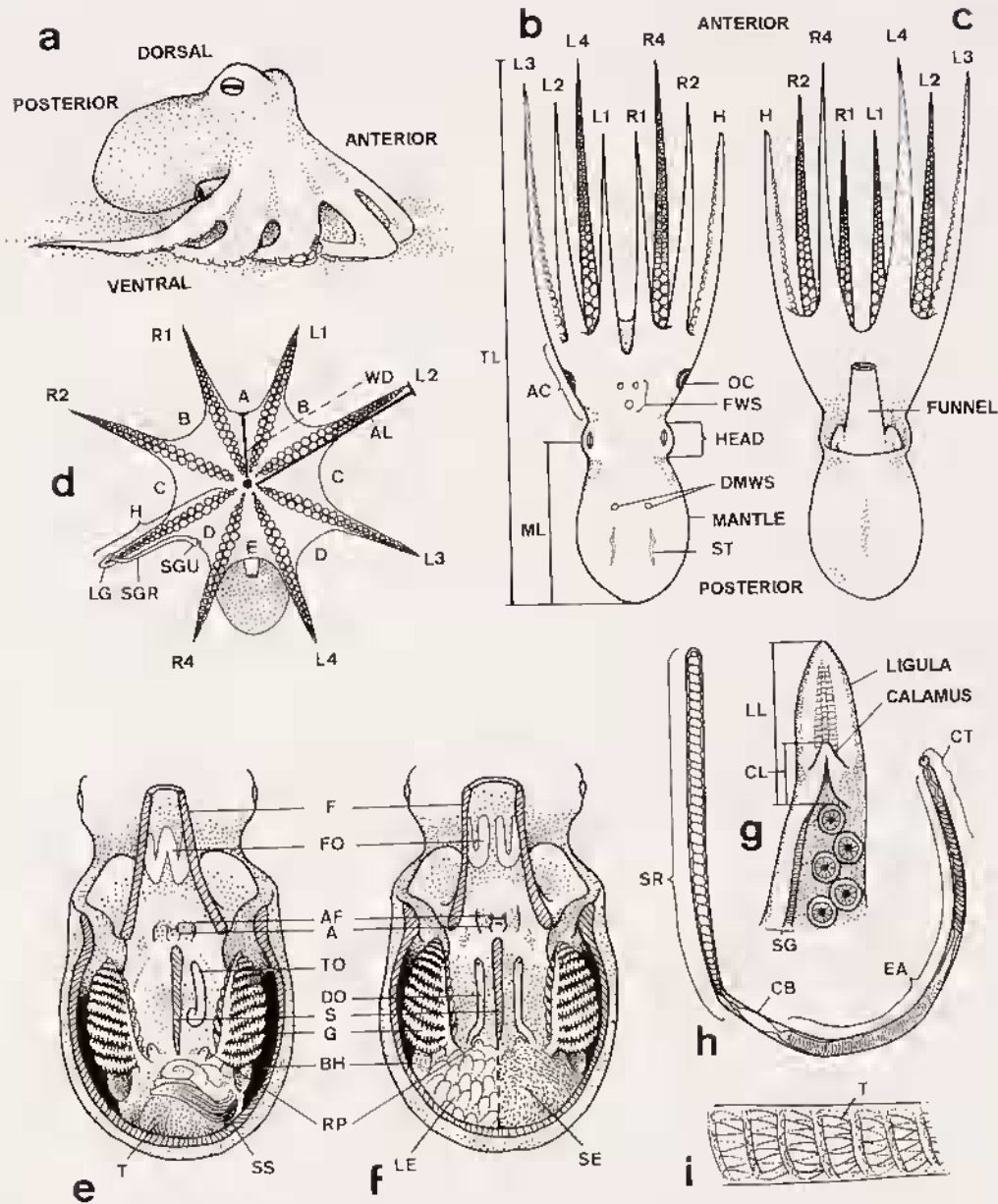


FIG. 1. — Orientation, terminology and measurements. L = left; R = right. — a, orientation relative to live animal. — b, whole animal, dorsal view. Arms numbered from dorsal to ventral as 1 to 4: AC = arm crown; DMWS = dorsal mantle white spots (*sensu* PACKARD & SANDERS, 1971); FWS = frontal white spots (*sensu* PACKARD & SANDERS, 1971); H = typical right-hand position of hectocotylysed arm in males (left hand in certain genera); ML = mantle length; OC = position of ocellus in ocellate octopuses; ST = position of stylets; TL = total length. — c, whole animal, lateral view. — d, oral view of arms and webs in males: AL = arm length; H = hectocotylysed arm; LG = ligula; SGR = spermatophore groove; SGU = spermatophore guide; WD = web depth. Webs designated from dorsal to ventral sectors by letters A to E. — e-f, mantle cavity contents: A = anus; AF = anal flaps; BH = branchial hearts; F = funnel; FO = funnel organ (W shape shown on male, UU shape shown on female); G = gills; S = septum; RP = renal papillae. — e, mantle cavity contents of mature male: SS = spermatophore storage sac; T = testis; TO = terminal organ ("penis"). — f, mantle cavity contents of mature female: DO = distal oviducts; LE = mature ovary as in "large-egg" species; SE = mature ovary as in "small-egg" species. — g, components of hectocotylysed arm tip of mature male: CL = calamus length; LL = ligula length; SG = spermatophore groove. — h, components of spermatophores: CB = cement body; CT = cap thread; EA = ejaculatory apparatus; SR = sperm reservoir. — i, midsection of ejaculatory apparatus in intact "armed" spermatophore of *O. aegina* showing inward pointing teeth (T).

State of maturity is divided into 3 stages: Immature (or juvenile), Submature and Mature. In immature material reproductive organs are not visible or tiny. Submature specimens have developed reproductive ducts (visible as distinct terminal organ or oviducts), but lack spermatophores or a swollen ovary. Mature females possess a large ovary, which occupies one-third or more of the mantle cavity and contains distinct individual eggs (shown for large- or small-egg species in Fig. 1f).

Diagnoses and descriptions presented here are based on submature and mature specimens. Data for juvenile material is not included as counts and relative measurements (such as sucker counts and arm lengths versus mantle length) undergo considerable ontogenetic change in the early growth stages and can cause overlap in otherwise valid diagnostic characters. Weights are presented for specimens preserved in 80% ethanol.

RESULTS

A total of 37 specimens of 6 species of octopods were collected from between 200 and 900 metres. Of these species, sufficient material for 5 species was available to enable description and treatment here, including 2 new species.

A single submature male (21.8 mm ML) of an additional species of the genus *Octopus* was encountered in material from KARUBAR station CP 84, off the Tanimbar Islands between 246 and 275 metres. It is distinct from the new species, *Octopus pyrum*, in possessing significantly shorter arms (~2 times mantle length) and a distinctive large pink leucophore on the posterior tip of the mantle. It lacks the diagnostic band of founder chromatophores found on the ventral mantle of *O. pyrum*. The submature state and poor condition of this specimen, however, prevents identification.

Additional material of 2 species collected from the same or adjacent regions were encountered in the collections of two Australian museums: the Northern Territory Museum in Darwin (NTM) and the Museum of Victoria, Melbourne (MV).

Species collected in the KARUBAR cruises and housed in the Muséum National d'Histoire Naturelle, Paris and the Pulitbang Oceanologi, Jakarta, are presented below, with depth ranges:

Family Octopodidae

<i>Benthoctopus karubar</i> sp. nov.	410-869 m
<i>Octopus pyrum</i> sp. nov.	329-511 m
<i>Octopus</i> sp. indeterminate	246-275 m
<i>Pteroctopus</i> sp.	205-620 m
<i>Eledone palari</i> Lu & Stranks, 1992	200-300 m

Family Alloposidae

<i>Haliphron atlanticus</i> Steenstrup, 1859	284-295 m
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SYSTEMATIC ACCOUNT

Family OCTOPODIDAE

Genus *BENTHOCTOPUS* Grimpe, 1921

Benthoctopus karubar sp. nov.

Figs 2-4, 11a

? *Benthoctopus* sp. C - ADAM, 1954: 186, fig. 37, pl. III, fig. 3.

MATERIAL EXAMINED. — Indonesia, KARUBAR, Kai Islands: stn CP 19, 576-605 m: 1 juv., 18.6 mm ML (MNHN 2063). — Stn CP 20, 769-809 m: 2 juv., 16.0, 17.1 mm (MNHN 2021).

Tanimbar Islands: stn CP 54, 836-869 m: 1 ♀, 70.9 mm ML (paratype MNHN 2038). — Stn CC 57, 603-620 m: 1 ♀, 96.8 mm ML (paratype MNHN 2049). — Stn CP 70, 410-413 m: 1 ♂, 59.6 mm ML (holotype MNHN 2026); 1 ♂, 51.0 mm ML (paratype POLIPI). — Stn CP 71, 477-480 m: 1 ♂, 46.0 mm ML (paratype MNHN 2027).

TYPE MATERIAL. — Holotype MNHN. Paratypes: 3 MNHN, 1 POLIPI. See above listing.

TYPE LOCALITY. — Off Tanimbar Islands, Arafura Sea, 08°41'S, 131°47'E, 410-413 m.

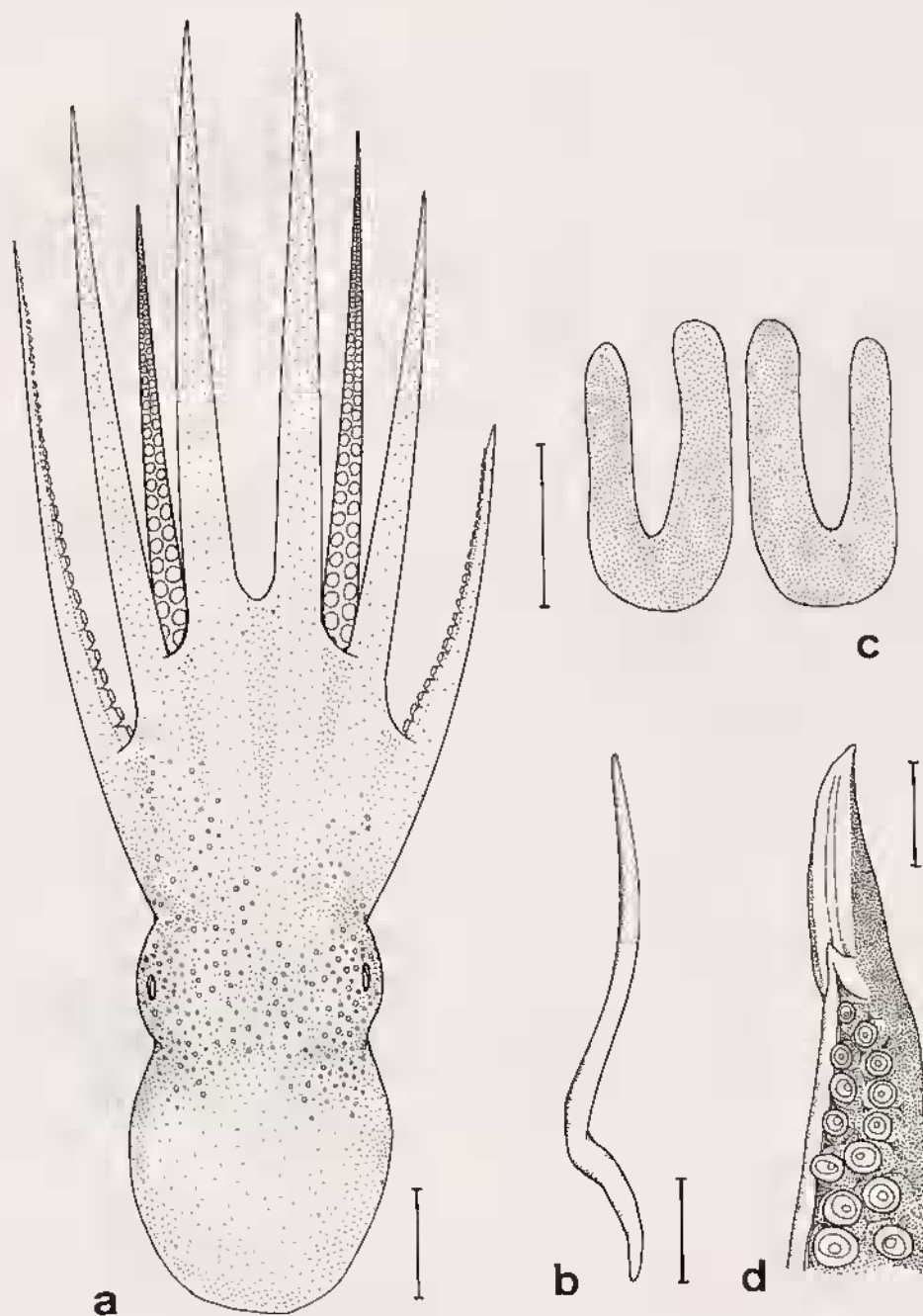


FIG. 2. — *Benthoctopus karubar* sp. nov. — a, dorsal whole animal, 59.6 mm ML male holotype (MNHN 2026). Scale bar = 20 mm. — b, stylet, 70.9 mm ML female (MNHN 2038). Scale bar = 5 mm. — c, funnel organ, 51.0 mm ML male, paratype (POLIPI). Scale bar = 5 mm. — d, ligula, holotype. Scale bar = 5 mm.

DIAGNOSIS. — Large species, ML to at least 100 mm. Arms short to moderate, around 2-3 times ML. Dorsal arms slightly longer than other arms. Webs deep, >33% of longest arm, approximately equal in length, ventral web slightly shallower. Suckers moderate sized, 7-10% of ML, forming two rows. Sucker counts to around 100 in males, 150 in females on normal arms, 47-55 on hectocotyliised arm of males. Enlarged suckers absent in both sexes. Funnel organ UU-shaped. Gill count 8-9 lamellae per demibranch. Ink sac and anal flaps absent. Hectocotylus on right third arm. Ligula large (>10% of arm length in mature males), pointed with an open

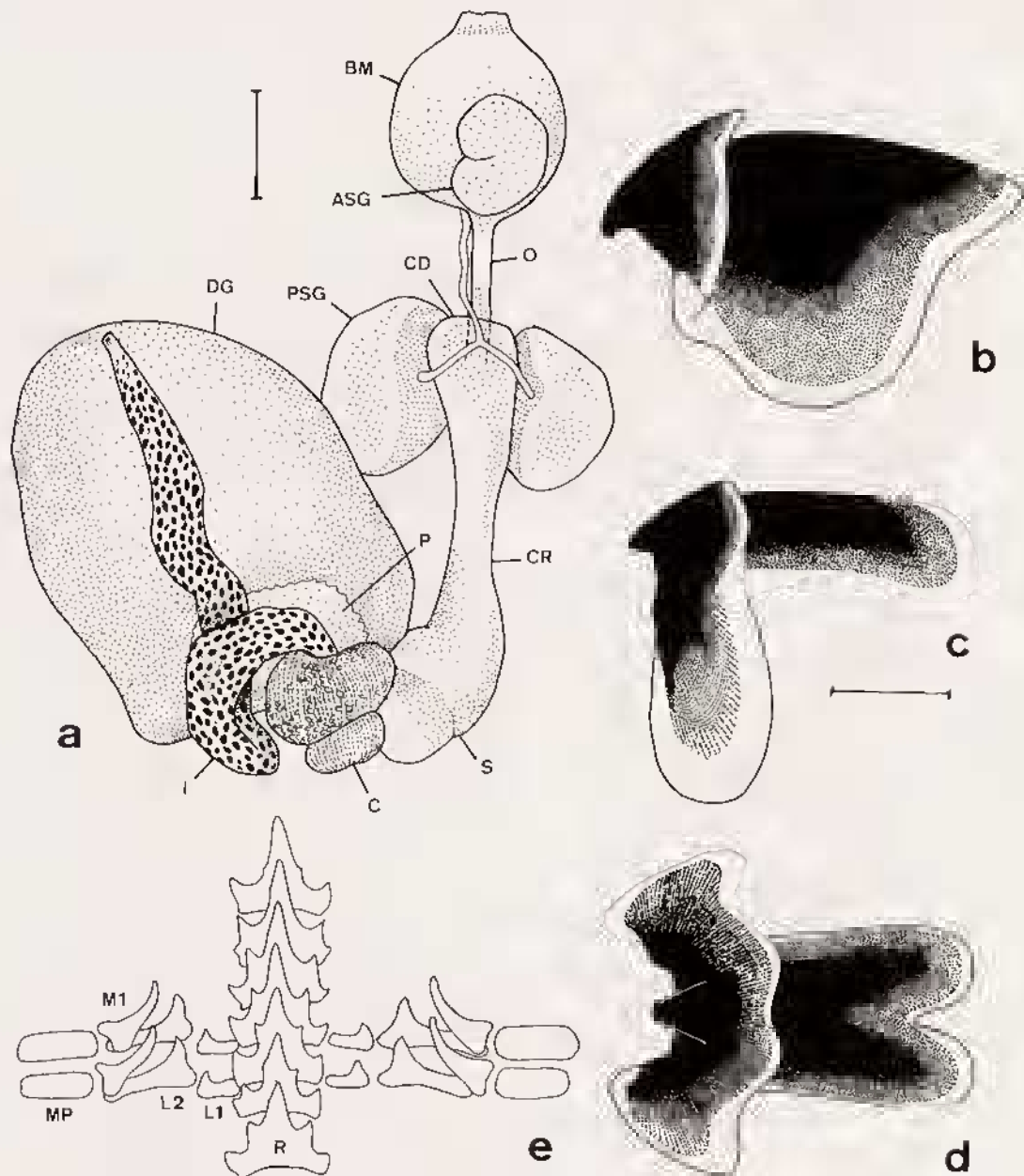


FIG. 3. — *Benihoctopus karubar* sp. nov. — a-e, digestive components of 70.9 mm ML female (MNHN 2038): a, digestive tract: ASG = anterior salivary gland; BM = buccal mass; C = caecum; CD = crop diverticulum; CR = crop; DG = digestive gland; I = intestine; O = oesophagus; P = pancreas; PSG = posterior salivary gland; S = stomach. Scale bar = 10 mm. — b, lateral view of upper beak. Scale bar for all beaks = 5 mm. — c, lateral view of lower beak. — d, ventral view of lower beak. — e, radula: R = rhachidian tooth; L1 = first lateral tooth; L2 = second lateral tooth; M1 = first marginal tooth; MP = marginal plate.

shallow groove. Calamus small and pointed (around 25% of ligula length). Spermatophores of moderate length (40.5mm, 70% of ML), produced in moderate numbers (26 in storage sac of holotype). Eggs large. Colour pattern: Pink to purple on all surfaces. Oral web dark purple. Skin sculpture: scattered with small low round papillae over dorsal head and some of mantle.

DESCRIPTION. — Counts and measurements are presented in Table 2 (p. 380). Data presented below is presented as ranges and means (latter in italics) for four KARUBAR specimens (1 mature and 1 submature male, 2 submature females).

Large species (Figs 2a, 11a); mantle length to at least 100 mm, total length to at least 400 mm; weight to at least 750 g. Mantle round to ovoid, longer than wide (width 48.0-74.4-97.7% of ML). Head wide (52.1-66.2-74.5% of ML, 72.1-91.9-108.6% of mantle width). Skin soft, semi-gelatinous in majority of specimens examined. Eyes large, slightly pronounced. Stylets present as thin and clear non-mineralized rods (Fig. 2b), length around 40% of ML. Mantle opening moderately wide, approximately 50% of circumference of body at level of opening. Funnel of moderate length, approximately 35% (30.8-34.7-40.6%) of mantle length, free portion approximately one-third (24.3-32.5-38.5%) of funnel length. Funnel organ UU-shaped (Fig. 2c), outer limbs approximately equal in length to median ones (outer limbs 96.8-98.7-102.2% of median limbs). Funnel organ occupies approximately 55% (54.1-56.7-59.2%) of funnel length.

Arms moderate length, around 2-3 times (2.2-2.7-3.1) mantle length. Arms robust, sub-cylindrical along length, tapering in distal third. Arm autotomy at base of arms absent. Arms approximately equal in length, dorsal lateral arms slightly longer. Suckers forming 2 rows and small to moderate sized, 7-10% of mantle length, slightly larger in female specimens (M: 7.6, 7.2; F: 9.9, 10.7% of ML). Enlarged suckers absent in both sexes. Up to 100 suckers on intact normal arms of males, up to 150 in females (maximums in males: 96, 102; females: 124, 146). Webs deep (deepest webs 33.1-35.4-37.7% of longest arm). Webs approximately equal in depth, ventral web shallower than other sectors.

Third right arm of males hectocotylised. Modified arm slightly shorter than opposite arm, approximately twice (1.7, 1.6 times) mantle length and around 80% (83.7, 72.7%) length of opposite arm. Ligula large (6.4 [in submature male], 13.3 [in holotype] % of arm length) and sharp (Fig. 2d). Ligula groove open. Floor of groove with medial rib lacking distinct transverse ridges. Calamus small and sharp, around 25% of ligula length (26.6% of ligula in holotype). Spermatophore groove well developed, wide and thin with fine transverse ridges. Spermatophore guide distinct, bordered by small ridges or digits of skin. Approximately 50 suckers on hectocotylised arm (47, 53 and 55 in three males).

Gills with 8-9 lamellae on both inner and outer demibranchs, plus terminal lamella.

Digestive tract illustrated in Fig. 3a. Anterior salivary glands large, longest dimension over 50% of length of buccal mass. Posterior salivary glands moderate sized (equal in length with buccal mass, approximately 40% of digestive gland length). Crop diverticulum well developed. Stomach bipartite. Caecum coiled to form more than 1.5 whorls, distinctly striated. Digestive gland approximately ovoid. Ink sac and anal flaps absent. Buccal mass, digestive gland and intestine covered in large purple chromatophores, potentially used as a means of masking light produced by bioluminescent prey. Beaks illustrated in Figs 3b-d. Upper beak with a short, slightly hooked rostrum and narrow hood (Fig. 3b). Lower beak with distinct rostrum, narrow hood and relatively parallel lateral walls separated in posterior 20% (Figs 3c-d). Radula with seven teeth and two marginal plates in each transverse row (Fig. 3e). Rhachidian tooth with 1-2 lateral cusps, typically 2, on each side of large medial cone. Lateral cusps in symmetrical to slightly asymmetrical seriation, migrating from lateral to medial position over approximately 6-7 transverse rows.

Male genitalia illustrated in Fig. 4a. Terminal organ ("penis") in mature males T-shaped with diverticulum distinctly longer than distal portion of organ. Spermatophores (Fig. 4b) of moderate length (40.5 mm, 67.9% of ML), produced in moderate numbers (26 in storage sac). Sperm reservoir under half spermatophore length (37.0%), containing thin sperm cord coiled in around 42 coils. Ejaculatory apparatus of spermatophore with 6-10 thin regular coils towards oral end.

Female genitalia illustrated in Fig. 4c. The largest female examined (96.8 mm ML, MNHN 2049) was almost mature and contained around 150 large eggs, reaching 14 mm long. One of the larger eggs showing follicular folds is illustrated in Fig. 4d.

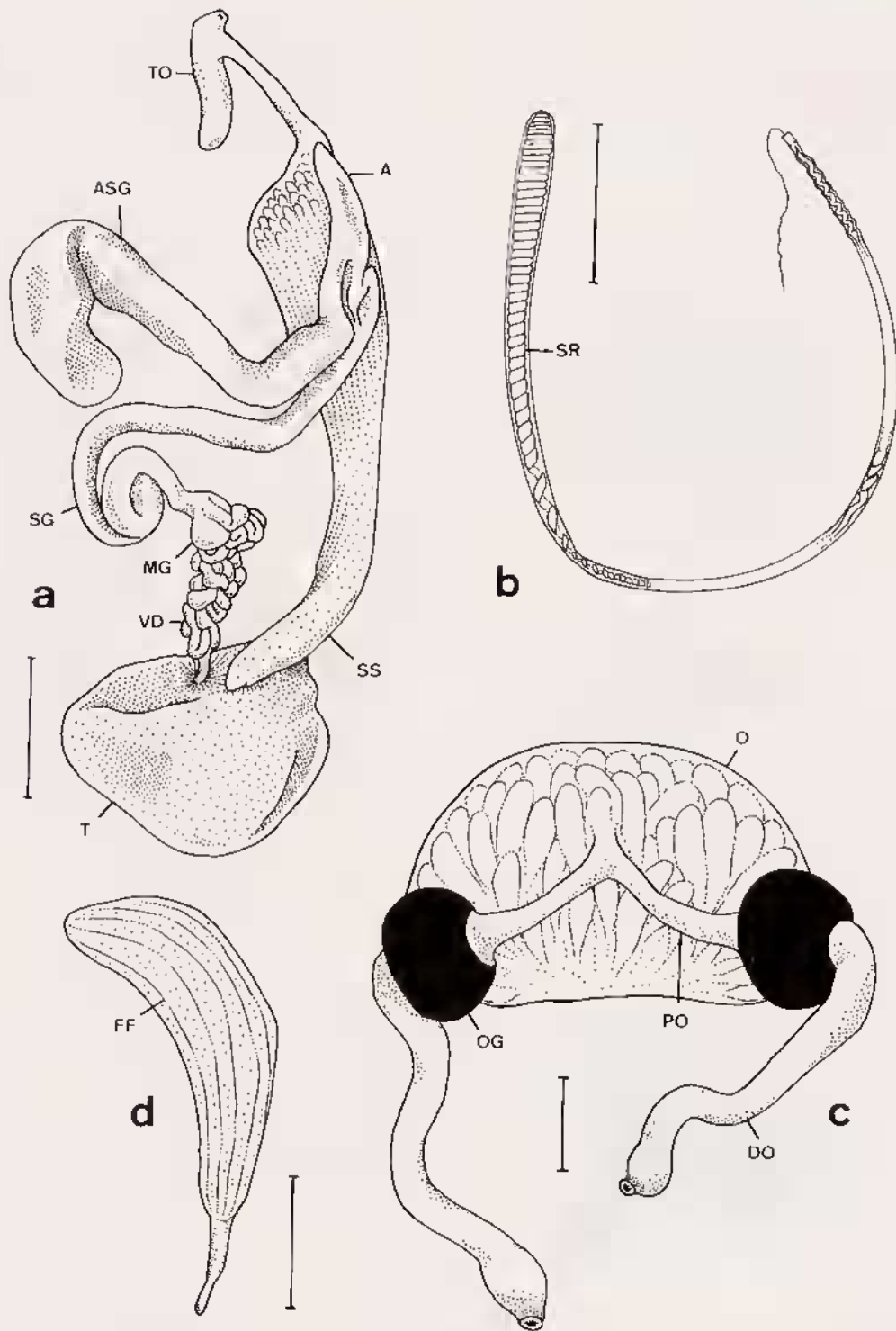


FIG. 4. — *Benthoctopus karubar* sp. nov. — a-b, male reproductive system of 59.6 mm ML holotype (MNHN 2026); a, reproductive tract: A = appendix; ASG = accessory spermatophoric gland; MG = mucilagenous gland; SG = spermatophoric gland; SS = spermatophore storage sac; T = testis; TO = terminal organ; VD = vas deferens. Scale bar = 10 mm. — b, spermatophore: SR = sperm reservoir. Scale bar = 5 mm. — c-d, female reproductive system of 96.8 mm ML female, paratype (MNHN 2049). — c, ovary: DO = distal oviduct; O = ovary; OG = oviducal gland; PO = proximal oviduct. Scale bar = 10 mm. — d, submature eggs showing follicular folds (FF). Scale bar = 5 mm.

Colour pattern of pink to dark purple colour produced by tiny crimson to purple chromatophores. Oral web dark purple in most specimens. Multiple (~8) irregular rows of subdermal founder chromatophores on arms. Little skin sculpture. Dorsal head and some of mantle scattered with small low rounded papillae (Fig. 2a). Lateral ridge absent.

REMARKS. — ADAM (1954) reported four specimens of *Benthoctopus* from the "Siboga" Expedition in Indonesian waters (in the region covered by the 1991 KARUBAR cruise), which he treated as 4 distinct undescribed taxa (species A-D). Collection depths ranged from 304 to 1886 m. Only ADAM's *Benthoctopus* sp. C, a female, shows similarities with the species described here, matching gill counts and radula dentition, and sharing similar arm lengths (longest 2.9 times mantle length), web depths (deepest 36% of longest arm) and dark skin colouration. ADAM provides no details of funnel organ shape.

ADAM's remaining species are distinct from *B. karubar*: *Benthoctopus* sp. A (female from 304 m) possesses a W-shaped funnel organ. *Benthoctopus* sp. B (male from 1886 m) has a distinctive radula with very large first lateral teeth (ADAM, fig. 36). *Benthoctopus* sp. D (female from 1158 m) possesses a much lower gill count, 5-6 lamellae per demibranch. *Benthoctopus* sp. C, collected from 794 m at 7°24'S, 118°15.2'E, was also the only specimen of the 4 to fall within the depth range of 400-800 m reported here for *B. karubar*.

As noted by NESIS (1987), the genus *Benthoctopus* is poorly studied. Most species are ill-defined with the proposed diagnostic characters often overlapping between taxa. Of the described species of *Benthoctopus*, only six species share with *B. karubar* a UU-shaped funnel organ and the absence of distinctly enlarged suckers in either sex. These taxa are compared to *B. karubar* in Table 3 (p. 380). The only described species close to the new species treated here is *B. levis*, described from the Antarctic waters surrounding Heard Island in the southern Indian Ocean. *Benthoctopus karubar* females lay large eggs (at least 14 mm long) and hence hatchlings would be benthic with limited capacity for dispersal. The distance between records for these 2 taxa, coupled with temperature differences between Antarctic waters and those of the Banda and Arafura Seas, are sufficient to consider these species distinct.

VOSS & PEARCY (1990) reviewed members of the genus *Benthoctopus* and described 5 new species from the north-east Pacific Ocean. All are distinct from *Benthoctopus karubar*, as all possess a W-shaped funnel organ.

The systematics of the genus *Benthoctopus* and its relationships with members of the genus *Bathypolypus* Grimpe, 1921 require significant revision. Members of the genus *Benthoctopus*, as it currently stands, are primarily grouped on the basis of a single character, the absence of a functional ink sac. It is likely that ancestral octopuses of different shallow-water lineages have been convergent in loss of the ink sac, as their ancestors shifted to lightless depths (where an ink sac offers no selective advantage). It is possible that this genus, as it currently stands, will prove to be polyphyletic.

ETYMOLOGY. — This species derives its names from the 1991 KARUBAR cruise, during which the known specimens were collected.

DISTRIBUTION. — *Benthoctopus karubar* is reported here from the Arafura Sea, Indonesia (near Kai and Tanimbar Islands). Material examined here was collected between 400 and 800 m.

Genus *OCTOPUS* Lamarck, 1798

Octopus pyrum sp. nov.

Figs 5-7, 11b

MATERIAL EXAMINED. — **Indonesia.** KARUBAR, *Kai Islands*: stn CC 10, 329-389 m: 1 ♂, 31.8 mm ML (holotype MNHN 2029); 1 ♂, 34.8; 2 ♀, 22.4, 29.9 mm ML (paratypes POLIPI).

Tanimbar Islands: stn CP 69, 356-368 m: 1 ♀, 29.1 mm ML, (paratype MNHN 2033); 1 ♀, 30.1 mm ML (MNHN 2208).

Australia. RV "Soela": stn SO6/85/27, off Townsville coast, 20°25.8'S, 152°57.7'E - 20°23.6'S, 152°57.7'E, 511 m, coll. CSIRO: 1 ♂, 22.9 mm ML (paratype MV F78818).

TYPE MATERIAL. — Holotype MNHN. Paratypes: 1 MNHN, 3 POLIPI, 1 MV.

TYPE LOCALITY. — Off Kai Islands, Banda Sea, 05°21'S, 132°30'E, 329-389 m.

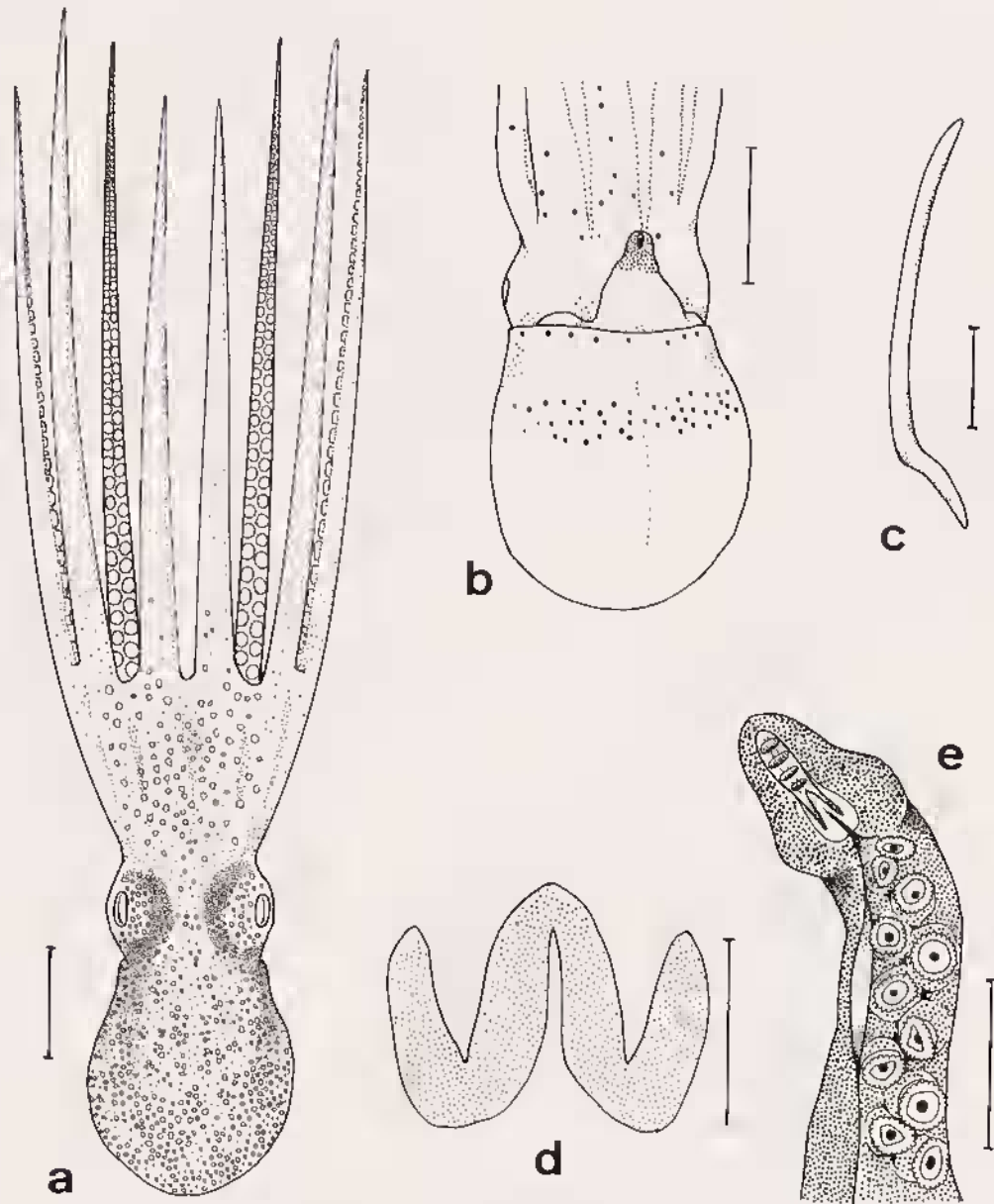


FIG. 5. — *Octopus pyrum* sp. nov. — a, dorsal whole animal, 29.1 mm ML female paratype (MNHN 2033). Scale bar = 10 mm. — b, ventral mantle, 22.4 mm ML female paratype (POLIPI). Scale bar = 10 mm. — c, stylet, 34.8 mm ML male paratype (POLIPI). Scale bar = 2 mm. — d, funnel organ, 31.8 mm ML male holotype (MNHN 2029). Scale bar = 5 mm. — e, ligula, holotype. Scale bar = 5 mm.

DIAGNOSIS. — Small to moderate size, ML to 35 mm. Arms moderately long, around 3-4 times ML. Arms approximately equal in length, lateral arms sometimes slightly longer than other arms. Webs moderately deep, deepest 20-30% of longest arm. Webs approximately equal in depth, lateral webs sometimes slightly deeper. Suckers small, 5.5-8% of ML, forming 2 rows. Sucker counts to around 120 on normal arms, 46-55 on hectocotylized arm of males. Enlarged suckers absent in both sexes. Funnel organ W-shaped. Gill count

7-8 lamellae per demibranch. Ink sac present. Hectocotylus on right third arm. Ligula large (8-10% of arm length), robust and pear-shaped with thickened sides to the ligula groove at the base. Calamus large and pointed (around 50% of ligula length). Spermatophores of moderate length (15-26 mm, 67-75% of ML), produced in low numbers (1-3 in storage sacs). Egg size unknown. Colour pattern: Orange to crimson base colour on dorsal surfaces, cream on ventral surfaces. Dorsal surfaces scattered with numerous raised leucophores, cream to gold in colour. Distinctive transverse band of around 50 founder chromatophores across midsection of ventral mantle. Large chromatophores on ventral digestive gland, visible within mantle cavity adjacent to gills. Skin sculpture: scattered with numerous raised round papillae over dorsal surfaces, including many over eyes.

DESCRIPTION. — Counts and measurements are presented in Table 4 (p. 381). The description below is based on 6 KARUBAR specimens (2 mature males and 4 submature females). Data is presented as ranges and means (latter in italics). Raw data for the Australian male specimen is also presented in Table 4 (see Remarks below).

Small to moderate sized species (Figs 5a, 11b); mantle length (ML) to at least 35 mm, total length to at least 170 mm; weight to at least 19 g. Mantle ovoid, longer than wide (width 55.2-71.7-87.9% of ML, 50.2% in slightly squashed Australian male). Head of moderate width (47.5-54.1-63.8% of ML, 67.0-76.7-86.9% of mantle width, 52.8% and 109.0% respectively for Australian male). Eyes large, slightly pronounced. Stylets present as thin and clear non-mineralized rods (Fig. 5c), length around 25% of ML. Mantle opening moderately wide, approximately 50% of circumference of body at level of opening. Funnel of moderate length, approximately 40% of mantle length (36.5-41.1-45.1% of ML, 36.7% in Australian male), free portion approximately half funnel length (42.2-47.5-52.3% of funnel length, 41.7% in Australian male). Funnel organ W-shaped (Fig. 5d), outer limbs shorter than median ones (outer limbs 71.4-76.8-82.5% of median limbs, 83.0% in Australian male). Funnel organ occupies approximately 50% of funnel length (45.0-51.7-57.9%, 55.9% in Australian male).

Arms of moderate length, around 3-4 times (2.8-3.2-3.9 x ML, 2.8 in Australian male) mantle length. Arms sub-cylindrical along length, tapering evenly along length to narrow tips. Arm autotomy at base of arms absent. Arms approximately equal in length, lateral arms sometimes slightly longer. Suckers small, less than 8% of mantle length in both sexes (5.5-6.8-7.6% of ML, 6.1% in Australian male), forming 2 rows. Enlarged suckers absent in both sexes. Up to 126 suckers on intact normal arms in submature and mature specimens (maximums 106 to 126 in material examined). Webs of moderate depth (deepest webs 19.4-22.6-27.8% of longest arm, 25.4% in Australian male). Webs approximately equal in depth, lateral webs slightly deeper in some specimens.

Third right arm of males hectocotylized. Modified arm short, approximately twice mantle length (1.8-2.0 times ML, 1.7 in Australian male) and around 65% length of opposite arm. Ligula large (8.0-10.0% of arm length, 8.8% in Australian male), robust and pear-shaped (Fig. 5e). Ligula groove deep with thickened lips near base forming pear shape. Floor of groove with medial rib and transverse ridges. Calamus large, narrow and sharp, around 50% of ligula length (45.3 and 55.8% of ligula in KARUBAR males, 51.4% in Australian male). Spermatophore groove well developed, wide and thin with fine transverse ridges. Spermatophore guide distinct, bordered by flattened papillae or digits of skin. Approximately 50 suckers on hectocotylized arm (46 and 55 in KARUBAR males, 47 in Australian male).

Gills with 7-8 lamellae on both inner and outer demibranchs, plus terminal lamella.

Digestive tract illustrated in Fig. 6a. Anterior salivary gland length approximately one third length of buccal mass. Posterior salivary glands large (almost as large as digestive gland). Crop diverticulum well developed. Stomach bipartite. Caecum coiled to form single whorl, distinctly striated. Digestive gland approximately ovoid with no evidence of pancreatic tissue. Ink sac present but small, partially embedded in ventral surface of digestive gland. Anal flaps present. Beaks illustrated in Figs 6b-d. Upper beak with a short, slightly hooked rostrum and narrow hood (Fig. 6b). Lower beak with worn rostrum in both dissected specimens (Fig. 6d), narrow hood, widely spread wings and flared lateral walls separated in posterior third (Fig. 6d). Radula with 7 teeth and 2 marginal plates in each transverse row (Fig. 6e). Rhachidian tooth with 1-2 lateral cusps on each side of large medial conc. Lateral cusps in asymmetrical seriation, migrating from lateral to medial position over 5-6 transverse rows.

Male genitalia illustrated in Fig. 7a. Terminal organ ("penis") in mature males T-shaped with diverticulum equal in size to distal portion of organ. Holotype with spermatophore within terminal organ, causing the diverticulum to stretch forming a plate-like portion (Fig. 7c). Spermatophores (Fig. 7b) of moderate length

(15-26 mm, 67-75% of ML), produced in low numbers (1-3 in spermatophore storage sac). Sperm reservoir under half spermatophore length (38.5%), containing fine to robust sperm cord (coiled in around 17 coils in partially discharged spermatophore of KARUBAR paratype, around 32 coils in better condition spermatophore of Australian male). Ejaculatory apparatus of spermatophore with irregularly placed segments, followed by a distinctive white cylindrical portion towards oral end.

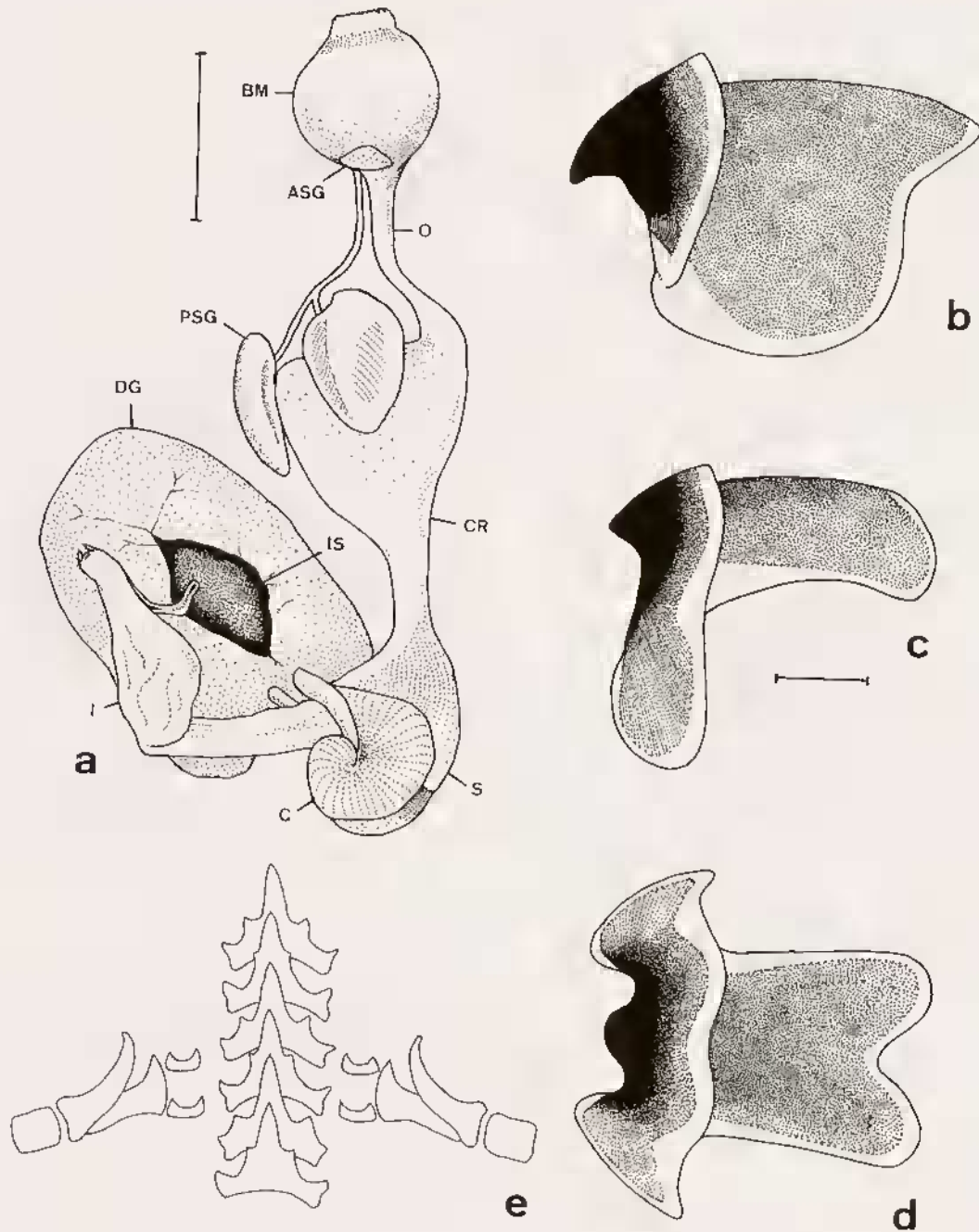


FIG. 6. — *Octopus pyrum* sp. nov. — a-e, digestive components, 34.8 mm ML male paratype (POLIPI): a, digestive tract. Symbols as in Fig. 3a, plus IS = ink sac. Scale bar = 10 mm. — b, lateral view of upper beak. Scale bar for all beaks = 2 mm. — c, lateral view of lower beak. — d, ventral view of lower beak. — e, radula.

No mature females were encountered in this study. Egg size and number unknown.

Basal colour pattern of orange to crimson on dorsal surfaces, cream on ventral surfaces. Dorsal surfaces covered in numerous round papillae, cream to gold in colour, colouration probably produced by fixed leucophores (Fig. 5a). Blue-black subdermal colour often visible over each eye. Ventral mantle with diagnostic transverse band of around 50 founder chromatophores at anterior third of mantle (Fig. 5b). Single row of founder chromatophores down midline of ventral arms. Large chromatophores also visible on ventral visceral envelope within mantle cavity, adjacent to gills (Fig. 7c).

Skin sculpture of loose granular texture formed by raised leucophore papillae over dorsal mantle, head, arm crown and arm bases. Lateral ridge absent.

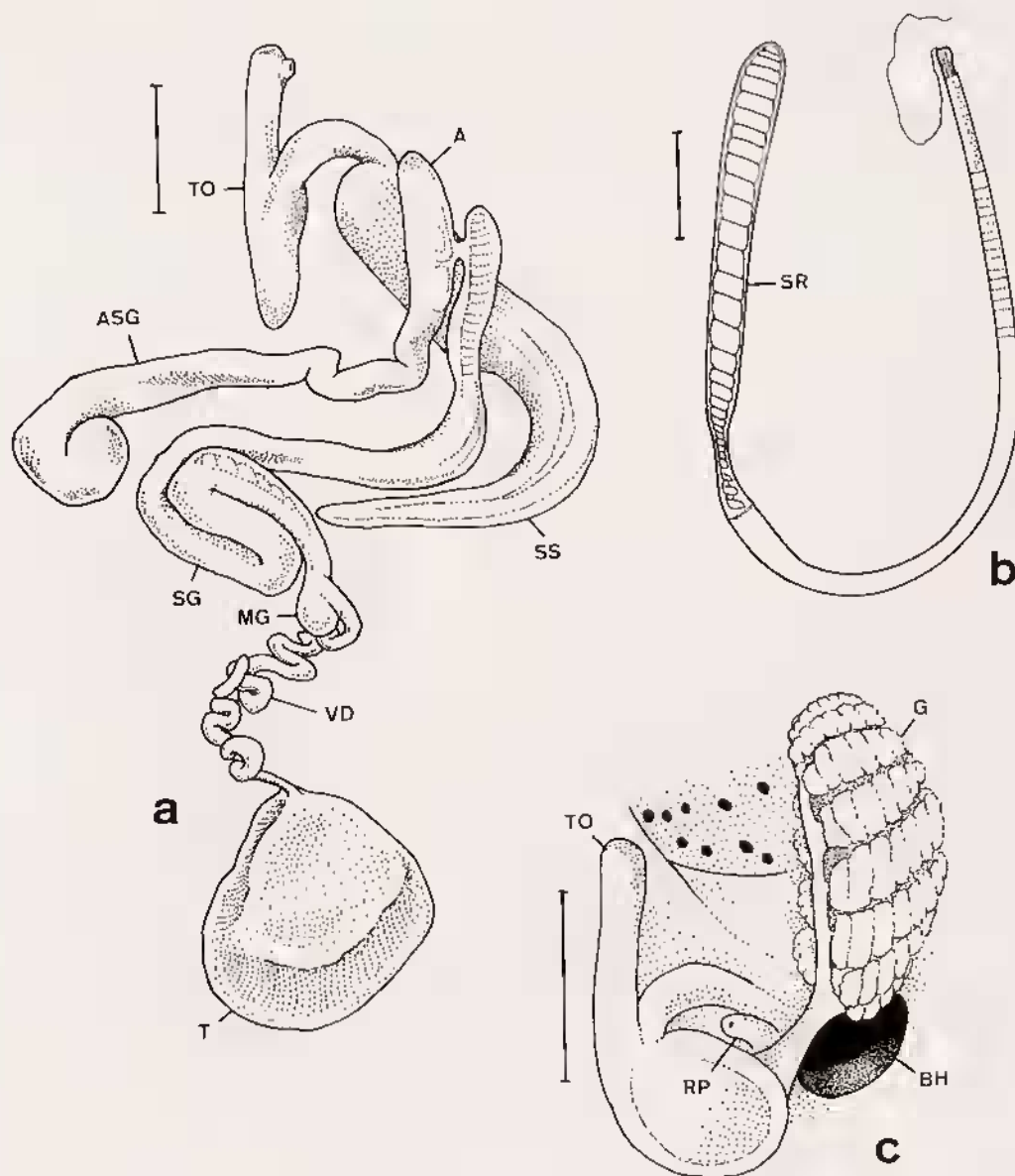


FIG. 7. — *Octopus pyrum* sp. nov. — a, reproductive tract, 34.8 mm ML male paratype (POLIPI). Symbols as in Fig. 4a. Scale bar = 5 mm. — b, spermatophore, holotype: SR = sperm reservoir. Scale bar = 2 mm. — c, terminal organ (TO), holotype: BH = branchial heart; G = gill; RP = renal papilla. Scale bar = 5 mm.

REMARKS. — The mature male specimen from off north-east Australia matched the Indonesian material in all characters and is accordingly included here. This specimen is slightly distorted but still possesses the diagnostic ligula, ventral mantle founder chromatophores, leucophores and matching sucker and gill counts.

There is only one recognised taxon which shows similarities with *Octopus pyrum*. The distinctive pear-shaped ligula with the swollen basal edges (Fig. 5e) shows some similarities with that of *Bathypolypus valdiviae* described by THIELE (*in* CHUN, 1915, pl. LXXX) from 500 m on the Agulhas Banks, off South Africa. These two taxa, however, are easily distinguished by the following characters in *B. valdiviae*: absence of an ink sac and crop diverticulum; a VV-shaped funnel organ; shorter arms (twice mantle length); deeper webs (33-40% of longest arm); larger ligula (13-18% of hectocotylized arm) and a radula with a rhachidian tooth which lacks lateral cusps.

ETYMOLOGY. — Derived from the Latin *pyrum* meaning "pear", which refers to the distinctive pear-shaped ligula of this species.

DISTRIBUTION. — *Octopus pyrum* is reported here from the waters of the Banda and Arafura Seas, Indonesia (from off the Kai and Tanimbar Islands) and north-east Australia (off Townsville, Queensland). Indonesian material was trawled from between 329-389 m, while the male specimen from off Townsville, Australia was collected from 511 m.

Genus *PTEROCTOPUS* P. Fischer, 1882

Pteroctopus sp.

Figs 8-10, 11c

MATERIAL EXAMINED. — **Indonesia.** KARUBAR, *Kai Islands*: stn CC 10, 329-389 m: 1 ♀, 50.3 mm ML (MNHN 2030). — Stn DW 18, 205-212 m: 1 ♀, 43.0 mm ML (MNHN 2019).

Tanimbar Islands: stn CC 57, 603-620 m: 1 ♀, 30.2 mm ML (MNHN 2064).

DIAGNOSIS. — Moderate sized species, ML to at least 50 mm. Small eye openings, broad head. Narrow mantle opening, less than 40% of circumference of body at level of opening. Arm lengths approximately 3 times mantle length. Arms approximately equal in length. Webs deep, >30% of longest arm length. Webs approximately equal in depth, lateral webs slightly deeper. Webs extend as membranous flared margins along entire length of arms, very well developed at arm tips. Suckers small, around 7% of ML, forming 2 rows. Sucker counts to around 150 in females on normal arms. Enlarged suckers absent in females. Large VV-shaped funnel organ. Gill count 8-9 lamellae per demibranch. Ink sac and anal flaps present. Eggs appear large-type in submature ovary. Colour pattern: crimson brown dorsally, pink ventrally. Skin sculpture: scattered with regular small round papillae over all dorsal surfaces. Two narrow elongate papillae over each eye.

DESCRIPTION. — Counts and measurements are presented in Table 5 (p. 381). Data presented below are raw data for the 2 larger KARUBAR females, both submature.

Moderate sized species (Figs 8a, 11c); mantle length to at least 50 mm, total length to at least 230 mm; weight to at least 110 g. Mantle ovoid, slightly flattened dorso-ventrally and longer than wide (width 77.4, 89.9% of ML). Head wide (64.7, 80.7% of ML, 83.5, 89.8% of mantle width). Skin soft, semi-gelatinous. Eyes moderate sized with small openings (Figs 8a, 8e). Stylets present as thin and clear non-mineralized rods (Fig. 8c), length around 40% of ML. Mantle opening narrow, less than 40% of circumference of body at level of opening (Fig. 8b). Funnel of moderate length, approximately 40% of mantle length (43.9, 35.1% of ML), free portion short, approximately 20% (22.6, 20.5%) of funnel length. Funnel organ VV-shaped (Fig. 8d), outer limbs approximately equal in length to median ones (outer limbs 87.1, 108.0% of median limbs). Funnel organ occupies approximately 40-50% (39.4, 56.3%) of funnel length.

Arms of moderate length, around 3 times (2.9, 3.3 x ML) mantle length. Arms moderately robust, sub-cylindrical along length, tapering in distal 20%. Arm autotomy at base of arms absent. Arms approximately equal in length. Suckers small, around 7% (6.3, 7.0%) of mantle length, forming 2 rows. Enlarged suckers absent in

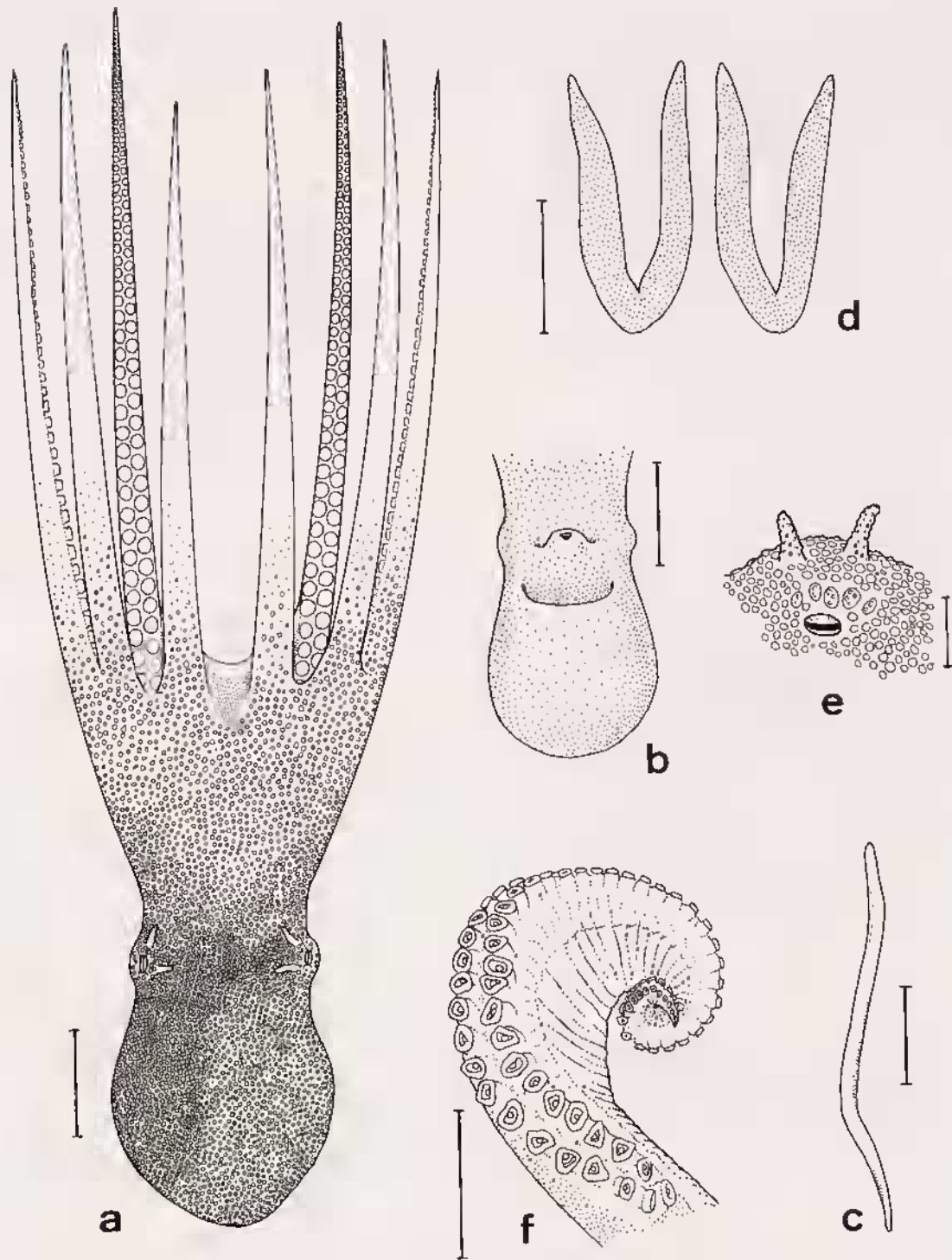


FIG. 8. — *Pteroctopus* sp. — **a**, dorsal whole animal, 50.3 mm ML female (MNHN 2030). Scale bar = 20 mm. — **b**, ventral mantle, 43.0 mm ML female (MNHN 2019). Scale bar = 20 mm. — **c**, stylet, 50.3 mm ML female (MNHN 2030). Scale bar = 5 mm. — **d**, funnel organ, 50.3 mm ML female, (MNHN 2030). Scale bar = 5 mm. — **e**, lateral view of head of 43.0 mm ML female (MNHN 2019), showing pair of papillae over each eye. Scale bar = 5 mm. — **f**, flared web margin on distal arms, 43.0 mm ML female (MNHN 2019). Scale bar = 5 mm.

females. Up to 150 suckers on intact arms of females (maximums in females: 144, 148). Webs deep (deepest webs 31.7, 36.3% of longest arm). Webs approximately equal in depth, laterals slightly deeper than dorsal and ventral webs. Webs extend as membranous flared margins along entire length of arms, very well developed at arm tips (Fig. 8f).

Gills with 8-9 lamellae on both inner and outer demibranchs, plus terminal lamella.

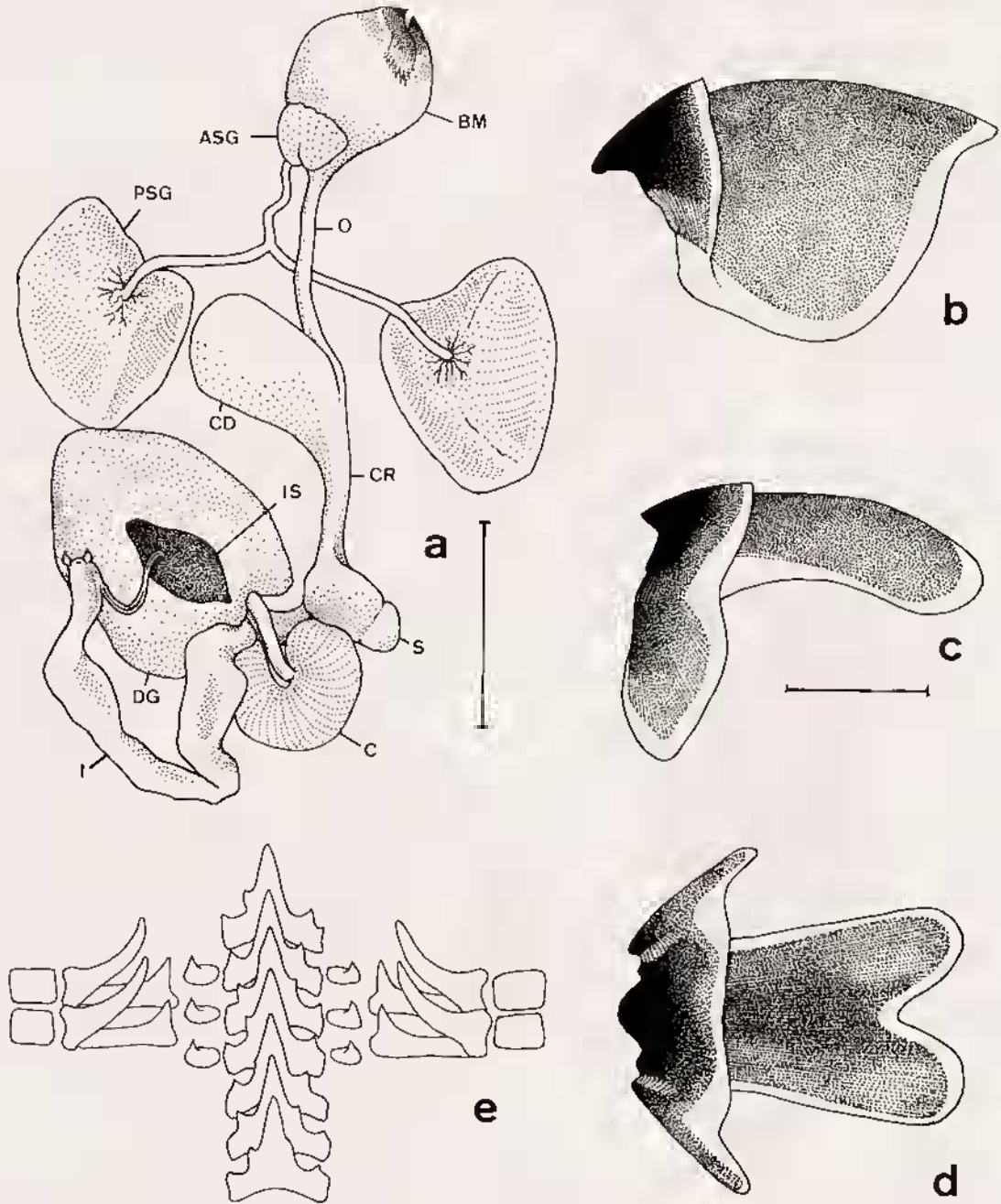


FIG. 9. — *Pteroctopus* sp. — a-e, digestive tract components of 43.0 mm ML female (MNHN 2019): a, digestive tract. Symbols as in Fig. 3a, plus IS = ink sac. Scale bar = 10 mm. — b, upper beak, lateral view. Scale bar for all beaks = 2 mm. — c, lower beak, lateral view. — d, lower beak, ventral view. — e, radula.

Digestive tract illustrated in Fig. 9a. Anterior salivary glands small, less than 20% of length of buccal mass. Posterior salivary glands moderate sized (longest dimension almost equal in length with buccal mass, approximately 40% of digestive gland length). Crop swollen, but not distinctly branched to form a diverticulum. Stomach bipartite. Caecum coiled in single whorl, distinctly striated. Digestive gland approximately ovoid. Ink sac and anal flaps present. Beaks illustrated in Figs 9b-d. Upper beak with a short, slightly hooked rostrum and moderate hood (Fig. 9b). Lower beak with rounded rostrum, narrow hood and relatively parallel lateral walls separated in posterior 15% (Figs 9c-d). Radula with 7 teeth and 2 marginal plates in each transverse row (Fig. 9e). Rhachidian tooth with 1-2 lateral cusps, typically 1, on each side of large medial cone. Lateral cusps in symmetrical seriation, migrating from lateral to medial position over approximately 4 transverse rows.

No males encountered in the KARUBAR cruise. A full description of male material from the Coral Sea and New Caledonia is in preparation.

Submature female genitalia illustrated in Fig. 10a. The larger female (50.3 mm ML, MNHN 2030) was submature with a small ovary, but possessed well-developed muscular distal oviducts. Eggs were forming in clusters throughout the submature ovary (Fig. 10b). These eggs are already 4 mm long in this small ovary and would thus be large-type eggs when mature (>10% of mantle length).

Basal colour crimson brown dorsally and pink ventrally, formed by tiny crimson chromatophores. Skin sculptured in numerous small rounded papillae in regular texture over all dorsal surfaces (Figs 8a, 11c). Few slightly larger bumps scattered over dorsal mantle. Two long papillae over each eye (Figs 8a, 8e). Lateral ridge absent.

REMARKS. — Considerable confusion surrounds a distinctive group of mid-depth octopuses, coined here as the *Pteroctopus/Danoctopus* complex, identified by the following diagnostic characters:

- muscular animals with loose, semi-gelatinous skin sculptured in small and regular low patches,
- distinctive narrow mantle aperture,
- VV-shaped funnel organ with narrow limbs,
- two narrow elongate papillae over each eye,
- flared web membranes extending to the arm tips, and
- a wide head with small eye apertures.

Members of this group occur in mid-depth habitats from around 100 to 1000 m in the Atlantic, Indian and Pacific

Oceans. Within this group are two separate subgroups, (1) those species treated under the genus *Danoctopus* Joubin, 1933 (and its synonyms *Berrya* Hoyle, 1939 and *Hapaloctopus* Taki, 1962) in which the hectocotylus of males is the third right arm; and (2) others treated under the genus *Pteroctopus*, where the third left arm of males is hectocotylised. A fifth nominal genus within this group, *Sasakinella* Taki, 1964 is based on a single female specimen from this group. As no males have been connected with TAKI's type specimen, the status of this generic name remains unresolved. NESIS (1987) recognised *Danoctopus*, *Pteroctopus* and *Sasakinella* as valid, though ill-defined, genera containing equally ill-defined species.

The 3 female KARUBAR specimens reported here clearly belong within this complex but were difficult to identify at both generic and species levels. The absence of male material prevented identification at the generic level, using the existing generic character of the side of the hectocotylised arm. Identification of these specimens was resolved on examination of material from comparable depths in the adjacent waters of the Coral Sea and New Caledonia, housed in MNHN. Amongst this material were numerous specimens from this group, including

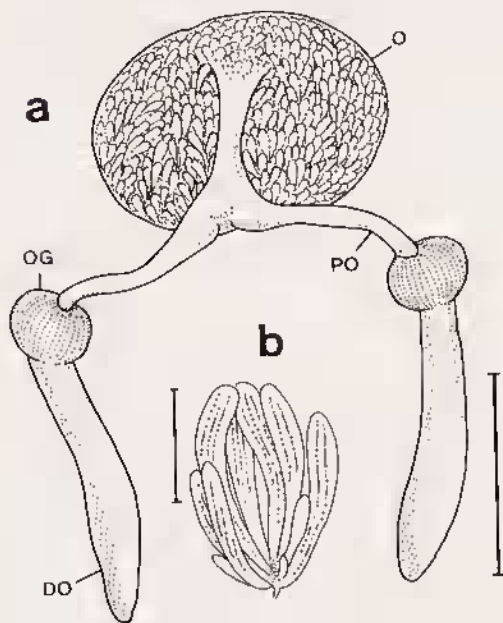


FIG. 10 — *Pteroctopus* sp.
a-b, reproductive system of 50.3 mm ML submature female (MNHN 2030): a, ovary. Symbols as in Fig. 4c. Scale bar = 10 mm. — b, cluster of immature ovarian eggs. Scale bar = 2 mm.

4 males, all with the third left arm hectocotylised. This attribute clearly identifies them as members of the genus *Pteroctopus* and constitutes the first record of this genus from tropical Indo-West Pacific waters. This material matched the KARUBAR females in counts, dimensions, skin sculpture and colour, and we consider them conspecific.

Only 2 species have been coined in the genus *Pteroctopus*, *P. tetracirrhus* delle Chiaje, 1830 (described from the Mediterranean Sea) and *P. witjazi* Akimushkin, 1963 (described from the Sea of Okhotsk, Russia, far northern Pacific). NESIS (1987) considers the differences distinguishing the latter species as minor and ill-defined. As a consequence of this lack of resolution, we have chosen to treat the taxon reported here as an indeterminate species of the genus *Pteroctopus*. Material from the Coral Sea and New Caledonia is currently being worked up and species level resolution for this taxon will be undertaken in that work.

The *Pteroctopus/Danoctopus* complex requires extensive revision, particularly development of characters which may aid to identify female specimens of all genera, as well as distinguish species within each member genus.

DISTRIBUTION. — KARUBAR material was collected off the Kai Islands, Banda Sea and Tanimbar Islands, Arafura Sea, between 205 and 620 m. Additional material discussed above from the Coral Sea and New Caledonia was collected between 383 and 600 m.

Genus *ELEDONE* Leach, 1817

Eledone palari Lu & Stranks, 1992

Fig. 11d

MATERIAL EXAMINED. — **Indonesia.** KARUBAR, *Tanimbar Islands*: stn CP 62, 246-253 m: 1 juv., 21.8 mm ML (MNHN 2034). — Stn CP 63, 214-215 m: 1 ♀, 32.6 mm ML (MNHN 2031). — Stn CP 78, 284-295 m: 1 ♀, 53.6 mm ML (MNHN 2024). — Stn CP 79, 239-250 m: 1 juv., 19.7; 1 ♂, 35.8; 1 ♀, 45.5 mm ML (MNHN 2020). — Stn DW 80, 199-201 m: 1 juv., 19.5 mm ML (MNHN 2058). — Stn CP 82, 215-219 m: 1 juv., 19.7 mm ML (MNHN 2067). — Stn CP 83, 285-297 m: 1 ♀, 64.5 mm (MNHN 2025). — Stn CP 84, 246-275 m: 2 juv., 19.3, 20.3; 1 ♀, 46.4 mm ML (MNHN 2035). — Stn CP 85, 240-245 m: 1 juv., 26.8; 1 ♀, 29.8; 1 ♂, 51.9 mm ML (POLIPI). — Stn CP 86, 223-225 m: 3 ♂, 44.6-54.2; 1 ♀, 62.8 mm ML (MNHN 2032).

Australia. Arafura Sea, Northern Territory, 9°46'S, 130°14'E, 270-300 m, 15 Sept. 1987: 1 ♀, 23.0 mm ML (NTM P1385).

DESCRIPTION (KARUBAR material). — The following brief description is based on KARUBAR specimens: 1 mature + 2 submature males, and 1 mature + 2 submature females. Counts and measurements for this material are presented in Table 6 (p. 382).

Moderate sized, robust octopuses (Fig. 11d), ML to 63 mm, wet weight to 120 g. Arms short, 1.5-2.0 times mantle length. Arm formula typically 1.2.3.4. Webs deep, 50-60 % of longest arm length. Webs decrease in depth from dorsal to ventral web. Suckers small, 5-7% of ML, forming a single row. Sucker counts, up to 50 in males, 76 in females. Hectocotylized arm of male (third right arm) with 44-45 suckers. No enlarged suckers in either sex. UU-shaped funnel organ. Gill count 5. Ink sac present. Ink duct opens anterior to opening of anus. Anal flaps absent. Ligula robust with large calamus. Tips of non-hectocotylized arms in males with spongiform tissue replacing suckers, modified portions up to 20% of arm length. Single spermatophore of mature male robust and armed with inward pointing teeth within ejaculatory apparatus. Sperm cord with ~15 cord whorls. Eggs large, up to 15 mm (~24% of ML), produced in low numbers. Colour pattern: pink cream-brown, to red-brown dorsally. White with scattered small crimson chromatophores on ventral surfaces. Skin sculpture: pairs of large papillae on dorsal mantle and arm crown, set within ring of smaller papillae. Lateral ridge well developed (Fig. 11d).

REMARKS. — The original description of the species by LU & STRANKS (1992) provided details of the morphology and distribution for this distinctive octopus. Additional notes on morphology, supplementing the earlier description, are provided below.

Stylets, the shell vestige of octopodids, are well developed in *Eledone palari*. They are keratin-like (non-mineralised) and approximately one-third of mantle length (21 mm in 62.8 mm ML female).

The inner margin of the mantle aperture is distinct from the form common to other members of the family Octopodidae. A well-developed flange on the posterior margin of the funnel corresponds with a matching deep fold inside the anterior edge of the ventral mantle. This structure is reminiscent of the flap-type mantle locking apparatus found in the pelagic octopods, *Tremoctopus violaceus* delle Chiaje, 1830 (Family Tremoctopodidae) and *Haliphron atlanticus* (Family Alloposidae).

Sucker counts on normal arms are low. Males possess up to 50 suckers proximal to the modified glandular tips. Females possess up to 76 suckers on the normal arms, which lack the glandular tissue found in the males.

Spermatophores are produced in low numbers (1-5 in storage sac) and are "armed". The inside of the ejaculatory apparatus is armed with sharp inward pointing teeth (as for example in Fig. 11i), which would splay out on the outer surfaces of the spermatophore on eversion. MANGOLD (1989) illustrated such armature in the intact and everted spermatophores of *Eledone cirrhosa* (Lamarck, 1798).

The generic status of this octopus requires review as it has a suite of morphological characters distinct from remaining species of the genus *Eledone*. All other members of the genus *Eledone* are restricted to the Atlantic Ocean and Mediterranean Sea.

DISTRIBUTION. — KARUBAR material was collected from east of the Tanimbar Islands in the Arafura Sea, between 8°S and 10°S, at depths of around 200 to 300 m. LU & STRANKS (1992) report the distribution of this species as the continental slope of Australia, from the Great Australian Bight, South Australia north to the southern Arafura Sea (~10°S), at depths between 110 and 620 m. All depth records reported by LU & STRANKS from shallower than 200 m are from cooler latitudes, south of 26°S.

Family ALLOPOSIDAE

Genus *HALIPHRON* Steenstrup, 1859

Haliphron atlanticus Steenstrup, 1859

Fig. 11e

Synonyms: *Alloposus mollis* Verrill, 1880; *Heptapus danai* Joubin, 1929. (See full synonymy in THORE, 1949).

MATERIAL EXAMINED. — KARUBAR, *Tanimbar Islands*: stn CP 78, 284-295: 1 ♀, 73.2 mm ML (MNHN 2046).

DESCRIPTION. — Counts and measurements are provided in Table 7 (p. 382). Mantle length 73.2 mm, total length approximately 300 mm, wet weight 165 g. Mantle round and semi-gelatinous with no constriction between the mantle and the head (Fig. 11e). Head broad, as wide as mantle. Eyes almost ventro-lateral in aspect. Mantle opening very wide, >60% of circumference at level of opening (Fig. 11e). Funnel-locking apparatus present as transverse flap on funnel, locking into corresponding crease on mantle wall. Arms short, longest 1.7 times ML. Arm formula unclear due to damaged arms in this specimen. Webs deep, >40% of longest arm length. Undamaged webs of similar depths. Suckers small, 6.0% of ML, first 6 suckers forming a single row from mouth to web margin, remaining suckers in 2 rows. At least 50 suckers on third arms, with 10-12 tiny suckers on tips. No enlarged suckers in single specimen. Large W-shaped funnel organ, lateral limbs equal in length with medial ones (Fig. 11e). Gill count 10 in outer demibranch, 9 in smaller inner demibranch. Ink sac and rudimentary anal flaps present with ink duct emerging anterior to opening of anus. Single female immature, reproductive tract not developed. Colour pattern: large pink chromatophores on smooth, loose and torn skin. Specimen coated in coagulated mucous and/or fine mud.

REMARKS. — We follow the works of KRISTENSEN & KNUDSEN (1983) and WILLASSEN (1986) in adopting the name *Haliphron atlanticus* Steenstrup, 1859 as senior synonym over the name *Alloposus mollis* Verrill, 1880.

THORE (1949) treated this taxon under the name *A. mollis*, reporting a large submature female (400 mm total length) from the Banda Sea (05°52'S, 131°14'E), close to the collection site for the KARUBAR specimen.

Our record is based on a single immature female, 73.2 mm in mantle length, ~300 mm in total length and weighing 165 grams. WILLASSEN (1986) reported two much larger females from off the coast of Norway, the largest being mature at a mantle length over 450 mm and weighing over 4.1 kg.

Little is known of the biology of this semi-gelatinous pelagic octopus. THORE discussed the funnel locking apparatus and muscular septa within the mantle cavity of this taxon, stating that "these septa give the impression that the power of expulsion of water from the mantle cavity must be great, thus making the animal a rather fast backward swimmer" (1949: 70). Fast jet propulsion may account for the scarcity of material captured in trawls compared with higher catches made of other, potentially slower, semi-gelatinous octopods such as *Japetella diaphana* Hoyle, 1885.

The habits of this species are not known. THORE (1949) captured specimens of this species between 20 and 350 m where the sea floor was over 2400 m deep. Other specimens have been collected in benthic dredges (VERRILL, 1882). Our specimen was collected in a beam trawl around 290 m, however the open net may have captured the animal as the net travelled through the water column. ALVARINO & HUNTER (1981) reported net avoidance in this species as observations of a young animal in surface waters fleeing ahead of the net, swimming faster than the towed net. The specimen was eventually captured enabling identification.

DISTRIBUTION. — The KARUBAR female was collected off the Tanimbar Islands, Arafura Sea. THORE (1949) reported the broader distribution of this species (under the name *Alloposus mollis*) as circumglobal in Atlantic, Indian and Pacific Oceans, between latitudes 40°N and 40°S.

DISCUSSION

Benthic octopuses reported here from the KARUBAR cruise to the Banda and Arafura Seas were collected between 199 and 869 m, from trawls between 100 and 1200 m. In these tropical latitudes, there appears to be a marked transition of the octopod fauna between shallow waters (< 200 m) and those of deeper waters. This faunal transition corresponds with temperature changes with depth. THORE (1949) presented temperature-depth profiles for tropical latitudes including stations within the Indo-Malayan Archipelago. THORE's data demonstrates a rapid drop in water temperatures from more than 25°C at the surface to around 13°C at 200 m. Temperature changes at greater depths are more gradual, dropping to around 10°C at 500 m and 8°C at 1000 m.

This faunal transition around 200 m is visible in the octopuses of northern Australia. Over 20 shallow-water species have been recognised from the waters of the Great Barrier Reef and northern Australia (NORMAN, 1993c). None of these species occur at depths greater than 185 m, despite considerable trawling activity at greater depths in the region. Trawls at depths over 200 m have encountered, instead, a distinct octopod fauna consisting of *Eledone palari* and at least 6 undescribed species (LU & STRANKS, 1992; NORMAN & LU, unpublished data).

The shallow-water octopuses of Indonesia have received little attention and require thorough revision. However, preliminary investigation of museum material collected from Indonesia has found a fauna consisting of the same species groups as found throughout the shallow waters of the Indo-Malayan Archipelago including northern Australia (see discussion of these species groups in NORMAN & SWEENEY, 1997).

The mid-depth octopuses reported here from the KARUBAR cruise show no affinities with the shallow-water faunas of either Indonesia or northern Australia. No members of the shallow waters species groups mentioned above are present in this fauna. The clear demarcation in composition and affinities between shallow and deeper faunas is reflected in a single specimen collected in the KARUBAR cruise from less than 200 m. One individual of an undescribed ocellate species of the genus *Octopus* (belonging in the shallow-water species group, the *O. aegina* group) was collected from 174-176 m (station CP 65, 09°14'S, 132°27'E, 1 Nov. 1991). This species was not encountered at greater depths.

The phylogenetic affinities of the mid-depth KARUBAR species are less clear. Members of the genus *Benthoctopus* are reported from throughout the world's oceans (NESIS, 1987). *Benthoctopus* requires extensive revision with most species placed in this genus solely on the basis of absence of an ink sac. As discussed above, it is premature to discuss phylogenetic affinities of *Benthoctopus* species.

The new species described here, *Octopus pyrum*, shows no affinities with any known shallow-water taxa. The distinctive pear-shaped ligula shows superficial similarities with that of *Bathypolypus valdiviae*, however the two species are distinct in a suite of other characters (see above).

As discussed above, the *Pteroctopus* species reported here belongs in the *Pteroctopus/Danoctopus* group, with members occurring in mid-depths (100-1000 m) throughout temperate and tropical latitudes of all oceans. The wide distribution of this group suggests an older lineage, potentially dating back to times of the circumglobal and equatorial Tethys Sea, potentially accounting for representation of this group in all oceans at these latitudes.

The anomalous *Eledone palari* shares a single row of suckers with the remaining members of the genus *Eledone*, all of which are restricted to the temperate and tropical waters of the Atlantic Ocean and Mediterranean Sea. It is distinct, however, in a number of morphological characters, including a different floorplan to the male reproductive tract, normal octopodid ligula and calamus, spongiform tissue on the modified arm tips of mature males, deep webs and distinct skin sculpture (regular paired papillae). The generic status of this species requires revision as it is likely to be distinct from the genuine *Eledone*, as represented in the Atlantic Ocean.

Eledone palari is restricted to the continental slopes surrounding the entire Australian land mass between 110 and 620 m. It produces large eggs (up to 15 mm) and as a consequence its hatchlings would be benthic in habit with limited capacity for dispersal. The geological stability and isolation of the Australian land mass over the last 350 million years (as it has travelled north from the fragmenting continent of Gondwana) may explain the distribution and unique nature of this taxon. It is possible that the ancestors of *E. palari* were carried north on this migrating land mass from southern polar waters, over sufficient time that direct ancestors of this unique octopus no longer exist. Conversely, the nearest relatives may prove to be the south polar genera *Bentheledone* Robson, 1932, *Thaumeledone* Robson, 1930 and *Megaleledone* Taki, 1961, all of which share a hectocotylus with well-developed calamus. All of these genera possess a single row of suckers and occur in deep and cold polar waters between 800 and 5300 m.

The reported circumglobal distribution of *Haliphron atlanticus* may reflect its pelagic habit. Nothing is known of the origins and phylogeny of this distinct animal.

Limited octopod material has been collected from greater depths (>1000 m) in tropical latitudes of the Indo-West Pacific region. The limited material collected from these depths includes benthic octopuses placed in the genus *Benthoctopus* Grimpe, 1921 (e.g., ADAM, 1954), pelagic gelatinous octopuses such as species of *Japetella* Hoyle, 1885, *Eledonella* Verrill, 1884 and *Vitreledonella* Joubin, 1918 (see THORE, 1949), and finned cirrate octopuses, such as *Grimptoteuthis pacifica* (Hoyle, 1885, collected from 4465 m).

The benthic octopod faunas which exist above and below 200 m in this tropical region hence appear phylogenetically distinct. These differences suggest that there have been no successful regional or recent descents of shallow-water lines into these darker cooler depths, at least within this region of the Indo-Malayan Archipelago. In order to further our knowledge of the nature and origins of these little known animals, further sampling, detailed morphological descriptions and appropriate molecular analyses are all required.

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TABLES

TABLE 1. — Summary of KARUBAR station data referred to in this paper.

KARUBAR Station N°	Latitude & Longitude	Depth (m)	Date (1991)	Local time	Species recorded
Kai Islands					
CC10	05°21'S, 132°30'E	329-389	23 Oct	10h55	<i>Octopus pyruui</i> sp. nov. <i>Pteroctopus</i> sp.
DW18	05°18'S, 133°01'E	205-212	24 Oct	20h22	<i>Pteroctopus</i> sp.
CP19	05°15'S, 133°01'E	576-605	25 Oct	06h40	<i>Benthoctopus karubar</i> sp. nov.
CP20	05°15'S, 132°59'E	769-809	25 Oct	09h53	<i>Benthoctopus karubar</i> sp. nov.
Tanimbar Islands					
CP54	08°21'S, 131°43'E	836-869	30 Oct	16h11	<i>Benthoctopus karubar</i> sp. nov.
CC57	08°19'S, 131°53'E	603-620	31 Oct	09h56	<i>Benthoctopus karubar</i> sp. nov. <i>Pteroctopus</i> sp.
CP62	09°01'S, 132°42'E	246-253	01 Nov	06h32	<i>Eledone palari</i>
CP63	09°00'S, 132°58'E	214-215	01 Nov	09h24	<i>Eledone palari</i>
CP69	08°42'S, 131°53'E	356-368	02 Nov	06h35	<i>Octopus pyruui</i> sp. nov.
CP70	08°41'S, 131°47'E	410-413	02 Nov	09h10	<i>Benthoctopus karubar</i> sp. nov.
CP71	08°38'S, 131°44'E	477-480	02 Nov	11h48	<i>Benthoctopus karubar</i> sp. nov.
CP78	09°06'S, 131°24'E	284-295	03 Nov	15h47	<i>Eledone palari</i> <i>Haliphron atlanticus</i>
CP79	09°16'S, 131°22'E	239-250	03 Nov	18h09	<i>Eledone palari</i>
DW80	09°37'S, 131°02'E	199-201	04 Nov	06h03	<i>Eledone palari</i>
CP82	09°32'S, 131°02'E	215-219	04 Nov	10h26	<i>Eledone palari</i>
CP83	09°23'S, 131°00'E	285-297	04 Nov	13h01	<i>Eledone palari</i>
CP84	09°23'S, 131°09'E	246-275	04 Nov	15h13	<i>Octopus</i> sp. indetermin. <i>Eledone palari</i>
CP85	09°22'S, 131°14'E	240-245	04 Nov	16h42	<i>Eledone palari</i>
CP86	09°26'S, 131°13'E	223-225	04 Nov	18h16	<i>Eledone palari</i>

TABLE 2. — Counts and measurements (raw data, measurements in mm) for 2 males and 2 females of *Benthoctopus karubar* sp. nov. D = damaged, H = hectocotylied arm.

Registration number	POLIPI	MNHN 2026	MNHN 2038	MNHN 2049
KARUBAR station:	CP70	CP70	CP54	CC57
Status	Paratype	Holotype	Paratype	Paratype
Sex	Male	Male	Female	Female
Maturity	late submature	mature	submature	late submature
Mantle length	51.0	59.6	70.9	96.8
Total length	174	243	301	422
Weight (g)	49.5	117.1	229.5	765.2
Mantle width	24.5	43.1	56.6	94.6
Head width	26.6	40.3	52.8	68.2
Shallowest web depth	ventral: 35	ventral: 35	ventral: 49	ventral: 82
Deepest web depth	dorsal: 41	dorsal: 55	dorso-lar: 74	dorsal 106
Arm lengths (L/R): 1	110 105	155 166	207 195	297 298
2	105 102	150 135	195 D	291 287
3	104 87H	128 93H	178 176	284 283
4	104 D	130 142	175 172	289 287
Sucker diameter	3.9	4.3	7.0	10.4
Sucker count: R3	55H	47H	124	139
L3	96	102	120	146
Ligula length	5.6	12.4	.	.
Calamus length	1.7	3.3	.	.
Spermatophore number	-	26	-	-
Spermatophore length	-	40.5	-	-
Spermatophore width	-	1.1	-	-
Sperm reservoir length	-	15.0	-	-
Sperm cord whorls	.	42	-	-
Egg number	-	-	submature	~150
Egg length	-	-	.	14
Egg width	.	-	-	4

TABLE 3. — Comparison of *Benthoctopus karubar* sp. nov. with similar described species. ALI = Arm Length Index, longest arm/mantle length. - LLI = Ligula Length Index, ligula length/hectocotylied arm length. - M = mature. - SDI = Sucker Diameter Index, largest sucker diameter/mantle length. - Sub = submature. - WDI = web depth index, depth of deepest web/ length of longest arm.

Species	Type locality	Depth (metres)	ALI (%)	LLI (%)	SDI (%)	WDI (%)
<i>Benthoctopus karubar</i> sp. nov.	Arafura Sea, Indonesia	400-800	2.2-3.1	6.3Sub	7-10	33-38
<i>B. ergasticus</i> (P. & H. Fischer, 1892)	North-east Atlantic	450-1500	3.3-6.7	13.3M	3.3-8	28
<i>B. fuscus</i> Taki, 1964	E of Honshu, Japan	Unknown	4.1	5	6.1	21
<i>B. januarii</i> (Hoyle, 1885)	Gulf of Mexico, NE Brazil	640	4-6	6-9	7.3	22
<i>B. levis</i> (Hoyle, 1885)	Heard Island, Indian Ocean (Antarctic)	137	2-3	7	6-8	33-40
<i>B. thielei</i> Robson, 1932	Kerguelen Is., Indian Ocean (Subantarctic)	Shore	2.2-2.7	13	9	25

TABLE 4. — Counts and measurements (raw data, measurements in mm) for material of *Octopus pyrum* sp. nov. D = damaged. - H = hectocotylized arm. - pd = sperm reservoir partially discharged.

Registration number	MNHN 2029	POLIPI	MV F78818	POLIPI	MNHN 2033	POLIPI	MNHN 2208
KARUBAR station	CC10	CC10	Australia	CC10	CP69	CC10	CP69
Status	Holotype	Paratype	Paratype	Paratype	Paratype	Paratype	-
Sex	Male	Male	Male	Female	Female	Female	Female
Maturity	Mature	Mature	Mature	Submature	Submature	Submature	Submature
Mantle length	31.8	34.8	22.9	22.4	29.1	29.9	30.1
Total length	148	174	92	101	120	128	120
Weight (g)	18.7	18.3	4.6	6.2	9.4	10.0	11.0
Mantle width	25.8	19.1	11.5	19.7	19.6	16.5	25.2
Head width	17.6	16.6	12.1	13.2	14.9	14.2	19.2
Shallowest web depth	22	22	12	17	15	14	18
Deepest web depth	lateral: 26	lateral: 26	dorso-lat: 16	lateral: 20	17	lateral: 19	20
Arm lengths (L/R): 1	100 98	105 104	D 61	58 62	78 75	63 76	75D 71
2	102 110	134 103	63 D	63 63	86 82	81 65D	83 81
3	101 65H	103D 64H	63 40H	72 68	79 81	91 87	79 84
4	102 85D	103 104	D 53	60 66	82 82	81 83	78 75D
Sucker diameter	2.4	2.4	1.4	1.7	1.6	1.9	2.0
Sucker count R3	55H	46H	47H	106	114	120	117
Sucker count L3	115	126	D	100	119	112	112
Ligula length	5.2	6.4	3.5	-	-	-	-
Calamus length	2.9	2.9	1.8	-	-	-	-
Spermatophore number	3	3	3	-	-	-	-
Spermatophore length	not dissected	26.0	15.4	-	-	-	-
Spermatophore width	-	1.0	0.9	-	-	-	-
Sperm reservoir length	-	10.0	5.7	-	-	-	-
Sperm cord whorls	-	~17pd	~32	-	-	-	-

TABLE 5. — Counts and measurements (raw data, measurements in mm) for two females of *Pteroctopus* sp. collected in KARUBAR cruise. D = damaged.

Registration number	MNHN 2019	MNHN 2030
KARUBAR station	DW18	CC10
Sex	Female	Female
Maturity	submature	submature
Mantle length	43.0	50.3
Total length	183	231
Weight (g)	37.3	113.2
Mantle width	33.3	45.2
Head width	27.8	40.6
Shallowest web depth	ventral: 22	dorsal: 30
Deepest web depth	lateral: 45	ventro-lateral: 53
Arm lengths (L/R): 1	124 116	147 153
2	120 101	160 D
3	105 104D	158 D
4	97 94D	167 D
Sucker diameter	2.7	3.5
Sucker count: R3	D	D
L3	144	148
Egg number	low	low
Egg length	large-type (submature)	large-type (submature)
Egg width	submature	submature

TABLE 6. — Counts and measurements (raw data, measurements in mm) for 3 males and 3 females of *Eledone palari*.
D = damaged. - H = hectocotylized arm.

Registration number	MNHN 2032	MNHN 2032	MNHN 2032	MNHN 2024	MNHN 2025	MNHN 2032
KARUBAR station	CP86	CP86	CP86	CP78	CP83	CP86
Sex	Male	Male	Male	Female	Female	Female
Maturity	Submature	Submature	Mature	Submature	Submature	Mature
Mantle length	44.6	46.6	54.2	53.5	64.5	62.8
Total length	124	128	152	154	178	170
Weight (g)	41.0	40.6	64.0	80.6	120.1	124.0
Mantle width	29.1	24.6	34.9	40.4	49.3	48.7
Head width	29.5	25.6	27.9	33.7	34.8	37.6
Shallowest web depth	ventral: 29	ventral: 27	ventral: 36	ventral: 40	ventral: 40	ventral: 50
Deepest web depth	dorsal: 42	dorsal: 41	dorsal: 45	dorsal: 50	dorsal: 62	dorsal: 59
Arm lengths (L/R) :1	74 76	71 75	90 91	91 89	104 97	101 98
2	74 64	68 70	80 81	90 83	98 90	90 94
3	72 53H	66 61H	82 65H	85 83	92 96	90 91
4	62 63	65 65	76 75	82 80	87 D	95 89
Male modified arm tip: 1	- 9	- 12	11 14	-	-	-
2	- 9	- 11	10D 13	-	-	-
3	- H	13 H	12 H	-	-	-
4	- 8	- 9	8 13	-	-	-
Sucker diameter	2.4	2.7	2.8	3.4	3.6	3.7
Sucker count R3	45H	44H	44H	72	76	74
Sucker count L3	50	46	48	73	74	71
Ligula length	2.7	3.0	3.6	-	-	-
Calamus length	1.5	1.8	2.2	-	-	-
Spermatophore number	-	-	1	-	-	-
Spermatophore length	-	-	25.1	-	-	-
Spermatophore width	-	-	1.2	-	-	-
Sperm reservoir length	-	-	10.1	-	-	-
Sperm cord whorls	-	-	~15 damaged	-	-	-
Egg number	-	-	-	submature	submature	25 mature
Egg length	-	-	-	-	-	20-30 immature
Egg width	-	-	-	-	-	15.0
						6.0

TABLE 7. — Counts and measurements (raw data, measurements in mm) for female of *Haliphron atlanticus*, KARUBAR Stn CP 78 (MNHN 2021). D = damaged.

Sex	Female
Maturity	submature
Mantle length	73.2
Total length	many arms D
Weight (g)	165.0
Mantle width	50
Head width	48
Shallowest web depth	dorsal: 35D?
Deepest web depth	ventro-lateral: 55
Arm lengths (L/R): 1	D D
2	D D
3	124 110
4	95 D
Sucker diameter	4.4
Sucker count: R3	50+
L3	54
Egg number	submature
Egg length	-
Egg width	-

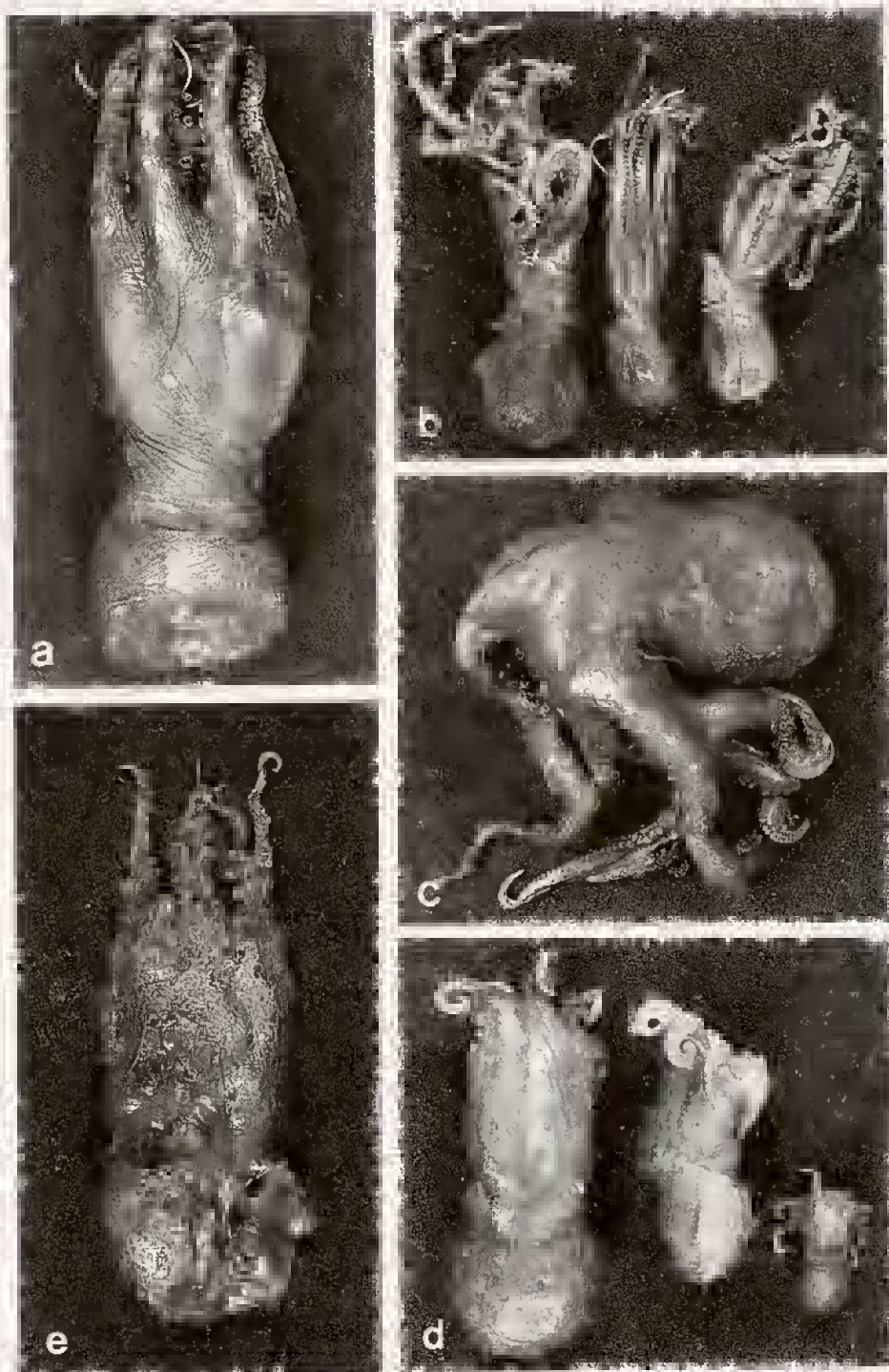


FIG. 11. — a, *Benthoctopus karubar* sp. nov. Dorsal view of 96.8 mm ML female, paratype (MNHN 2049). — b, *Octopus pyrum* sp. nov. From left: dorsal view of male paratype (34.8 mm ML, POLIPI) and ventral views of female paratype (22.4 mm ML, POLIPI) and male holotype (31.8 mm ML, MNHN 2029). — c, *Pteroctopus* sp. Dorsal view of 50.3 mm ML female (MNHN 2030). — d, *Eledone palari*. From left: dorsal view of 45.5 mm ML female, lateral view of 35.8 mm ML male, ventral view of 19.7 mm ML juvenile, (all MNHN 2020). — e, *Haliphron atlanticus*. Ventral view of 73.2 mm ML female (MNHN 2046). Mantle and funnel dissected open to display gills and funnel organ respectively.